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REPRODUCTIVE BIOLOGY OF LIZARDS ON THE AMERICAN SAMOAN ISLANDS

By
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The reproductive biology of most lizards is poorly known. This is particularly true for tropical species, and most especially for island populations in the Pacific region (Brown, 1956; Inger and Greenberg, 1966; Fitch, 1970; Duellman, 1978). This study concerns certain aspects of the reproductive biology of 12 species of lizards on the tropical Pacific islands of American Samoa. There are no published studies describing lizard reproduction on these islands. The species accounts presented herein summarize basic data on male and female sizes (snout-vent lengths) at reproductive maturity, clutch sizes, descriptions of eggs, incubation periods, and hatchling sizes. Data on some species are sufficient to suggest relationships between climatic variables and monthly frequencies of fecund and ovigerous females and to indicate patterns in annual reproductive activity. Reproductive modes for these and other species are summarized from the basic observations and discussed in terms of reproductive strategies (Tinkle, *et al.*, 1970; Duellman, 1978).

Limitations of data include: (1) size at maturity for males was estimated from measurements of testes lengths and the presence of enlarged convoluted tubules in freshly preserved specimens, not from sections or smears of testicular tissue from which the presence of viable sperm can be detected; (2) small samples for a few species do not always reflect the full range of snout-vent lengths from hatchlings to adults; and, (3) samples were not taken during all months of the year, and sample sizes for any given month represent the total collections from several habitats and islands.

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Previous studies have shown that monthly samples are essential for detecting annual reproductive cycles in temperate areas with marked fluctuations in mean monthly temperatures and rainfall (Fitch, 1954, 1956; Fitch and Greene, 1965; Mount, 1963; Tanner, 1957; Tinkle, 1961, 1967; and others). Similarly, monthly samples are necessary in equatorial tropical areas where temperatures remain relatively constant, but where fluctuations in precipitation apparently dictate corresponding seasonality in the reproductive conditions of lizards (Sexton, *et al.*, 1971; Fitch, 1973; Ruibal, *et al.*, 1972; Brown and Sexton, 1978; Andrews and Rand, 1974; Gorman and Licht, 1974; Crump, 1974; and, Duellman, 1978). Alternatively, reproductive patterns in lizards are relatively aseasonal in areas where both temperatures and rainfall are constant year round (Inger and Greenberg, 1966). I will demonstrate the marked constancy of annual temperature and rainfall in American Samoa and present correlations among these variables and other climatic parameters with the monthly frequencies of reproductive activity among certain lizard species. Following the evidence of Inger and Greenberg (1966), if annual climatic patterns are relatively constant, there should be little seasonality in the reproductive activity of lizards in American Samoa.

In discussing the reproductive strategies of lizards in American Samoa, I recognize Wilbur, Tinkle and Collins's (1974) list of components to a life history study. These are clearly summarized in Duellman (1978) as follows: (1) mortality schedules of juveniles and adults, (2) age at first reproduction, (3) reproductive life-span, (4) fecundity (including number and size of eggs, frequency of deposition, and proportion of females breeding), (5) the fecundity-age regression, (6) degree of parental care, and (7) reproductive effort. My data partially satisfy components 2, 4, 5, 6 and 7, but are insufficient for the others.

As an index of reproductive effort I have used the ratio of clutch weight (wet weight of oviducal complement in preservative) over total, wet body weight and converted the mass ratios to caloric ratios using the formula of Vitt (1978), $C_c/C_t = 1.2905\ (WW_c/WW_t) + 0.0640$, where C_c/C_t is the caloric ratio (clutch calories/total body + clutch calories), WW_c is wet weight of clutch, and WW_t is wet weight of total body + clutch. These indices and the evidence for annual reproductive activity are compared among certain coexisting species of *Emoia* in American Samoa. The results are discussed in terms of the two generally recognized reproductive strategies in lizards (Tinkle, *et al.*, 1970; Duellman, 1978): (1) early maturing species with annual multiple broods, and (2) late maturing species with single broods annually. Three (non-exclusive) views attempting to account for the evolution of these strategies are (1) that early maturing species with multiple clutches are primarily tropical, oviparous taxa with smaller clutch sizes adjusted by higher intraspecific competition (Tinkle, *et al.*, 1970), (2) that more frequent and smaller clutches in tropical lizards (notably *Anolis*) is an adaptation to their more arboreal habits (an argument extended to the family Gekkonidae, numerous arboreal species of which almost always have one or two egges per clutch, Andrews and Rand, 1974), and (3) that body shape, foraging activity, escape mechanisms and other aspects of lizard ecology predict clutch size in ecologically similar species (Vitt and Congdon, 1978). Duellman (1978) offered a more balanced view and equated overall reproductive effort for species with low clutch sizes and multiple broods and species with high clutch sizes and single broods, depending on the overall survivorship of eggs, young, and gravid females, annually, in any given environment. His view is that the two reproductive strategies have general correlations with aseasonal and seasonal environments, respectively, but that numerous exceptions reflect differences in complexity of the overall environment of the individual species, which in turn affects all of the components suggested by Wilbur, *et al.*, (1974).

Data for the species in American Samoa presented herein offer interesting comparisons with these views, for, although relatively few species are found on these islands, the lizard fauna has been assembled from non-endemic, rafting colonizers with notably different ecologies (Schwaner, 1979).

MATERIALS AND METHODS

The distribution of lizards in American Samoa is discussed by Amerson, *et al.*, (1978), and Schwaner (1979); major collecting localities for specimens reported herein may be found in these references. The twelve species in American Samoa are non-endemic, widespread lizards on islands throughout the Pacific area and elsewhere. Some species are among those lizards with the greatest known geographic distributions.

A total of 2047 specimens was examined during this study; individual reproductive data was obtained by dissection of preserved material. Field caught individuals were preserved in 10% formalin and later transferred to 70% ETOH. External measurements were taken with vernier calipers or a millimeter rule on preserved specimens only (except for a small series of *Emoia cyanura* which were weighed on a 5 gm Pesola spring balance in the field prior to preservation). Snout-vent length to the nearest 0.5 mm was measured ventrally as the distance from the anterior edge of the cloaca to the tip of the snout. The body cavity was opened by midventral or lateral incision and the following data recorded: (1) sex, (2) reproductive condition of ovaries and oviducts, or testes, (3) number and length (greatest diameter) of all developing ova, oviducal eggs, and testes to the nearest 0.1 mm, and (4) wet weight (to the nearest 0.1 gm) of the entire clutch complement and combined weight of clutch and body of ovigerous females.

Reproductive status was judged as: (1) *immature,* for hatchlings and males with small, undeveloped testes (< 2.0 mm), lacking convoluted tubules, or females with small whitish ova (usually less than 1.0 or 2.0 mm in size) and narrow oviducts, (2) *maturing,* for males with slightly enlarged testes (> 2.0 mm), lacking well developed convoluted tubules, and for females with enlarged, yellowish, developing ova (fecund), without noticeably distended oviducts, (3) *mature,* for males with enlarged testes and convoluted tubules, and females with oviducal eggs (ovigerous), and (4) *old mature,* for males in similar condition to (3), but with greatly enlarged and vasculated testes, and for females with greatly enlarged oviducts, and small developing ova (recently spent). These categories are rather arbitrarily defined, but, they facilitate an orderly separation of males and females into age (size) classes of recognizable reproductive condition.

Clutches of eggs, when found in the field, were placed in loosely tied plastic bags with some of the substrate on which they were found; if the nest material was moist, it was occasionally sprinkled with water so as to maintain moisture levels during incubation of the eggs. For gecko eggs the nesting substrate was usually dry, so eggs were loosely covered in dry paper toweling before placing in plastic bags. Laboratory temperatures during incubation approximated ambient air temperatures in shade during the day (24°-26°C), and were probably slightly lower than those in the field. Most hatchlings were photographed and preserved immediately, but some *(Emoia nigra)* were maintained alive on a diet of small insects for several weeks to ascertain changes in color pattern.

RESULTS

Emoia nigra

This large diurnal skink was caught on the ground (where it forages widely), and on tree trunks (where it basks) within 3 m of the ground. At night I found two individuals, one under a rock and another in an epiphytic fern about 2 m from the forest floor.

Males.—The 194 specimens have snout-vent lengths of 41-121 mm (Fig. 1). Individuals less than 80 mm generally have small, whitish testes (usually below 5.0 mm in length) lacking enlarged convoluted tubules. Testes sizes for individuals with snout-vent lengths greater than 90 mm deviate noticeable upward (exponentially) from a regression line fitted to individuals less than 90 mm in length (Fig. 2; $Y = 0.11 X - 3.90$, $r = .53$, $p < .001$). Testes of most individuals above 90 mm are heavily convoluted and highly

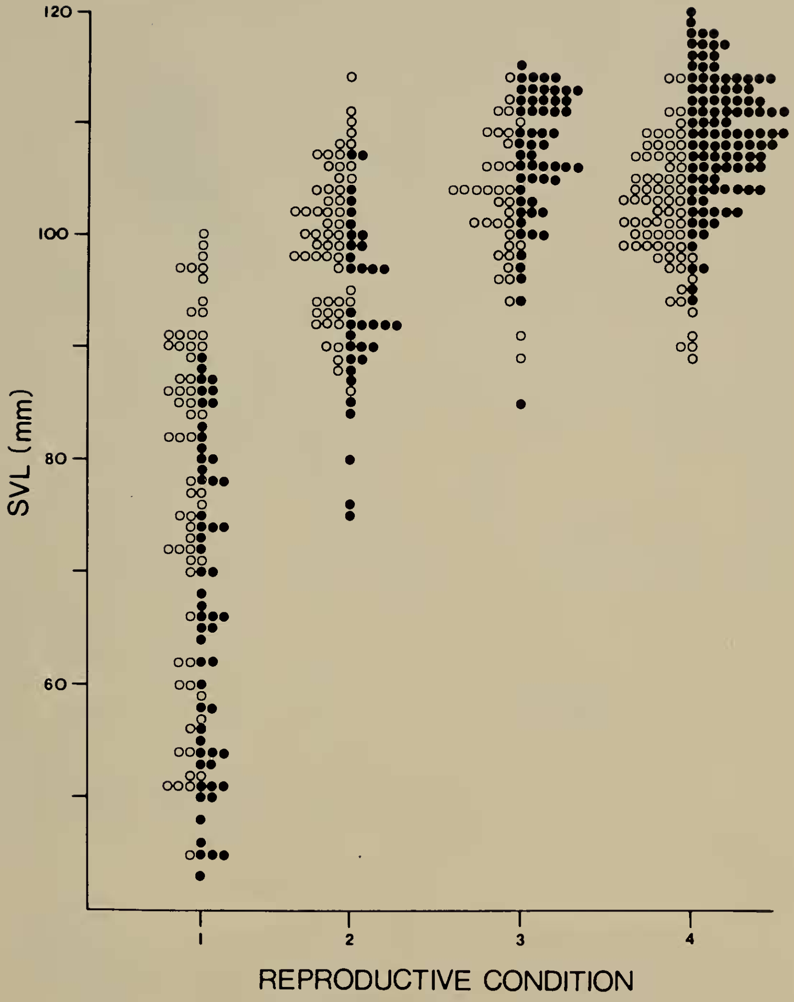

FIG. 1.—Reproductive condition and snout-vent length (SVL in mm) of *Emoia nigra* from islands of American Samoa. Reproductive conditions: (1) immature, (2) maturing, (3) mature, (4) old mature (see text for further explanation). Solid circles are males; hollow circles, females.

vasculated. Males with enlarged testes were found during all month of the study indicating that they are reproductively active throughout the year.

Females.—Of 223 females having snout-vent lengths of 42-114 mm, the smallest fecund female (developing ova > 5.0 mm) is 86 mm and the smallest with oviducal eggs, 89 mm (Fig. 1). Thus the size at sexual maturity for female *E. nigra* appears to be 86-89 mm.

Mean clutch size, based on 86 fecund and 31 ovigerous females,

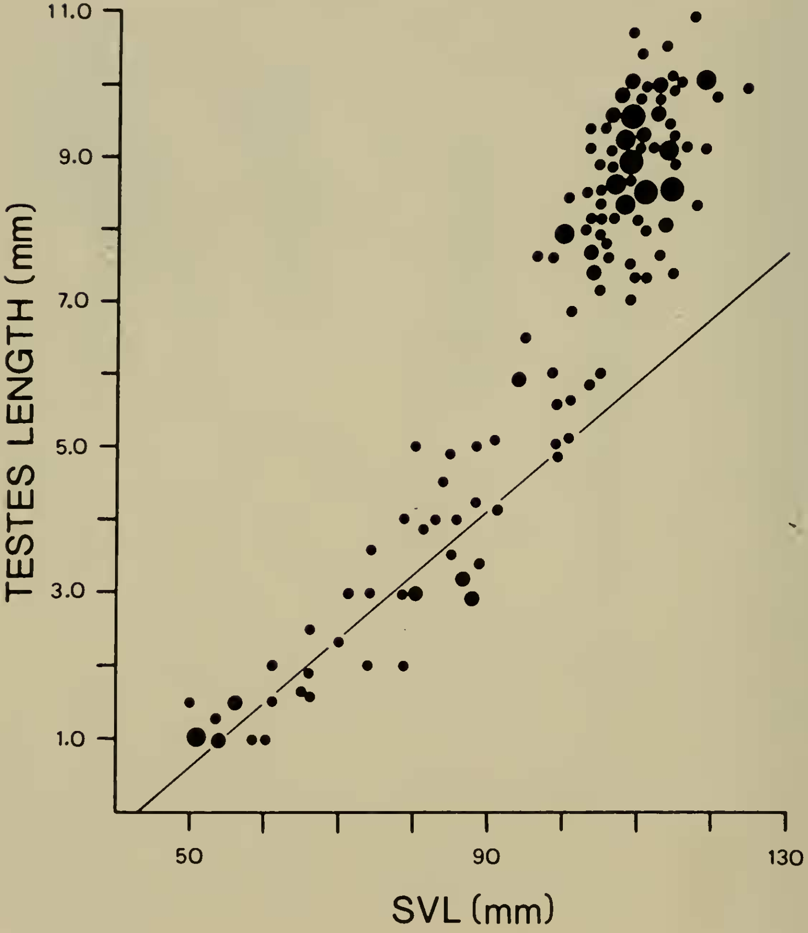

Fig. 2.—Testes length versus snout-vent length (in mm) for male *Emoia nigra* from American Samoa. Dots form a size gradient representing one (smallest) to five (largest) individuals. Regression line fitted by least squares method to data points below 90 mm SVL.

and three clutches found in the field, is 2.32 (range = 2-4). There is a slight, but non-significant increase in clutch size with female snout-vent length (Fig. 3A). A few large females (> 100 mm SVL) had only one egg (all with thick leathery shells) and could have laid an egg or two just prior to capture. These data confirm Greer's (1968) note on clutch sizes of 10 gravid *E. nigra*. The diameters of 84 oviducal eggs measured 13.5-22.1 mm ($\bar{X}$ = 19.0 mm) and closely approximated the length x width of freshly laid eggs ($\bar{X}$ = 19.2 x 13.5 mm, range = 18.0-20.0 x 12.5-15.0 mm, n = 7).

Incubating eggs of *E. nigra* swell in size, presumably by absorbing water, and are 3-4 mm larger in length and width ($\bar{X}$ = 22.0 x

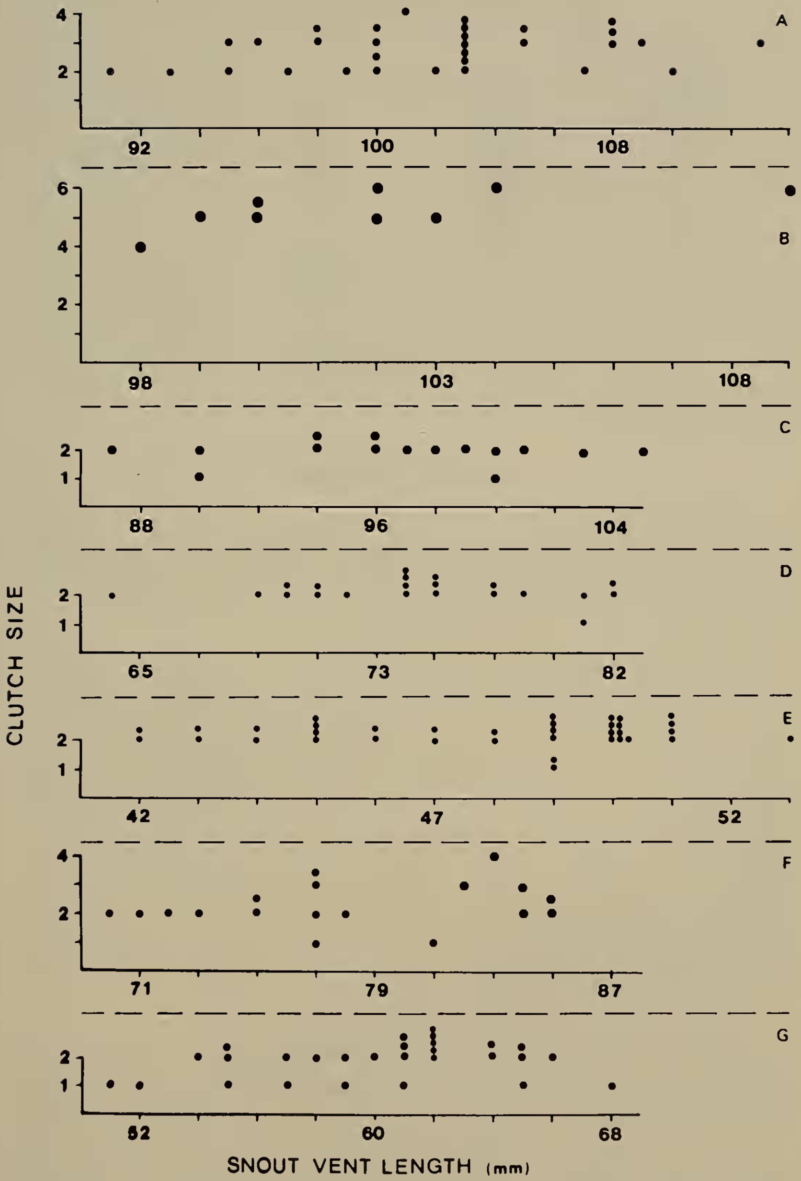

FIG. 3.—Clutch size versus body size for (A) *Emoia nigra*, (B) *E. samoense*, (C) *E. lawesii*, (D) *E. adspersa*, (E) *E. cyanura*, (F) *Gehyra oceanica*, (G) *Crytodactylus pelagicus* from islands of American Samoa. Clutch size based on ovigerous and fecund females. Dots represent individual lizards.

18.0 mm, n = 7) at hatching than at partuition. Eggs not placed on moist soil or paper toweling shriveled and failed to hatch under laboratory conditions.

Three clutches of eggs were taken from a birdnest fern (*Asplenium nidis*, Polypodiaceae) and under rotting stumps of coconut trees. Times from collection to hatching are 30-65 days; as a conservative estimate, two months is probably the usual incubation time for eggs in the field.

Hatchlings have snout-vent lengths 34.0-41.0 mm ($\bar{X}$ = 39.1, n = 10) and differ markedly from juveniles and adults in color pattern (Schwaner, 1979). In one hatchling reared in the laboratory, the pattern began to change in about two weeks and after three weeks the individual was indistinguishable in color pattern, although smaller in size, from most juveniles and young adults collected in the field.

Emoia samoense

This large diurnal skink was caught primarily on tree trunks and in low vegetation (where it forages and basks) from near ground level to several meters above the ground. None was observed at night, but several individuals were seen perched in trees at sunrise and sunset.

Males.—The 116 specimens have snout-vent lengths of 66-118 mm (Fig. 4). Individuals less than 90 mm generally have small whitish testes (below 4.0 mm in length) lacking enlarged convoluted tubules; specimens 90-100 mm snout-vent length have slightly enlarged testes. Reproductively active males greater than about 95 mm snout-vent length deviate noticeably upward from a regression line fitted to individuals less than 95 mm in length (Fig. 5; $Y = 0.1X-4.78$, $r = .63$, $p < .001$). Testes sizes for individuals above 95 mm snout-vent length cluster near 8.0-9.0 mm; thus, males probably mature about 90 mm snout-vent length. Males with enlarged testes were found during all months of the study, suggesting that reproductive activity probably is year round.

Females.—Of 81 females having snout-vent lengths of 71-114 mm, the smallest fecund female (developing ova > 4.0 mm) is 84 mm and the smallest with oviducal eggs, 95 mm (Fig. 4). Thus, the size at sexual maturity of female *E. samoense* is probably 84-95 mm.

Mean clutch size, based on 20 fecund and 10 ovigerous females, is 5.3 (range = 4-7). There is a significant increase in number of oviducal eggs with female snout-vent length ($r = .68$, $p < .05$, Fig. 3B). Greer (1968) examined a single gravid *E. samoense* with 5 oviducal eggs. The diameters of 58 oviducal eggs measured 8.6-14.5 mm ($\bar{X}$ = 12.3 mm); average egg length x width at partuition is 14.5 x 9.5 mm (range = 14.0-15.0 x 9.0-10.0 mm, n = 2). These eggs also swell in size during incubation; at hatching one egg meas-

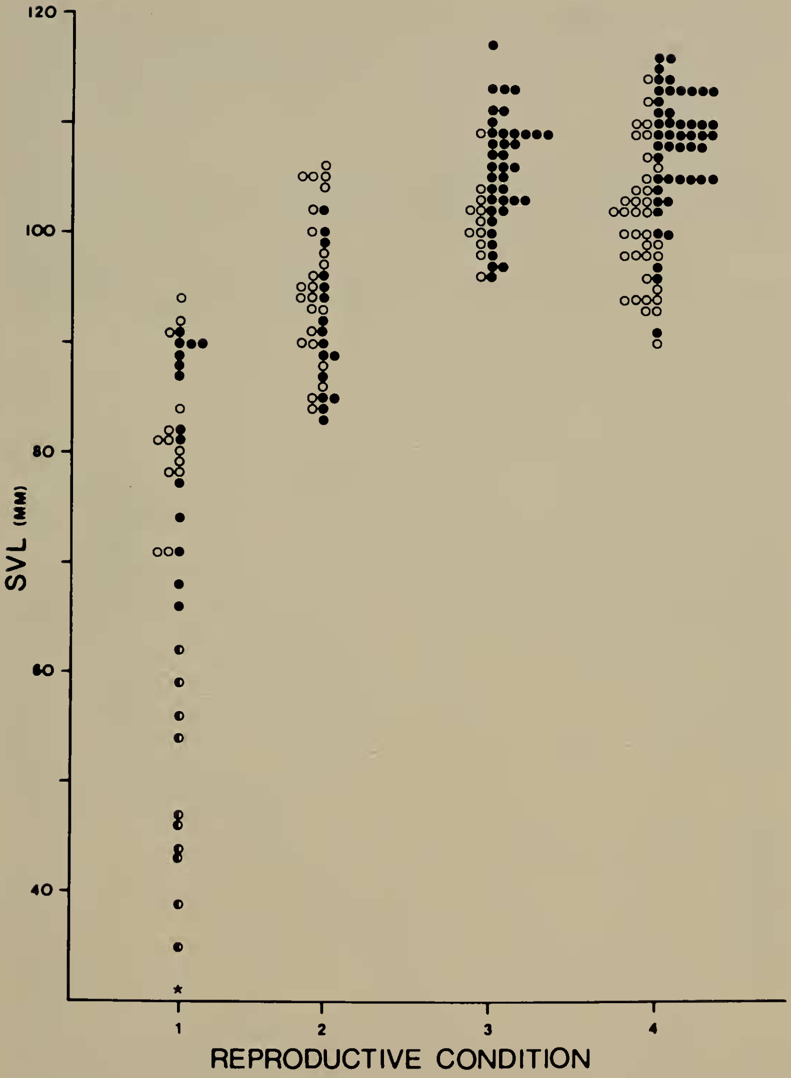

FIG. 4.—Reproductive condition and snout-vent length (in mm) of *Emoia samoense* from islands of American Samoa. Half-shaded circles are juveniles; star is a hatchling. Other symbols are as in Fig. 1.

ured 15.5 x 10.5 mm. Eggs of *E. samoense* have distinct longitudinal striations running along the external surface of the shell.

Hatchlings of *E. samoense* have never been reported. A single *E. samoense* egg found with a clutch of two larger eggs of *E. nigra* in a birdnest fern in mangrove swamp hatched 44 days after discovery. This incubation time is probably only slightly less than the true incubation period. The hatchling snout-vent length is 31.0 mm.

Whether or not the one discovered egg represents single placement of eggs by *E. samoense* cannot be concluded. Captive females have laid one or two eggs in laboratory cages and withheld the rest for several days or weeks. However, none of these eggs developed, and most were thin shelled and probably laid prematurely. A field observation with anecdotal implications, was made at the time of discovery of the single *E. samoense* egg. Moments after the collection, a gravid *E. nigra* was captured from an adjacent mangrove tree. Upon dissection she was found to have three oviducal eggs and three *E. samoense* eggs in her stomach and intestines. Perhaps

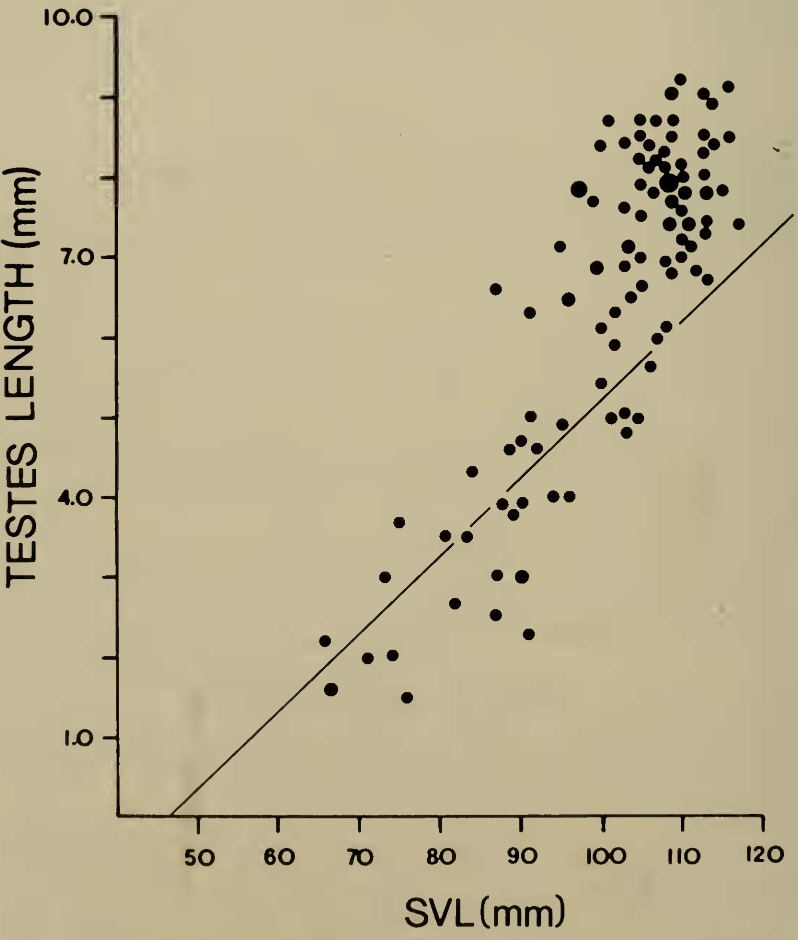

FIG. 5.—Testes length versus snout-vent length (in mm) for male *Emoia samoense* from American Samoa. Symbols are as in Fig. 2. Regression line fitted by least squares method to data points below 95 mm SVL.

these eggs were from the clutch found in the birdnest fern. The presence of other lizard eggs in stomachs of *E. nigra* individuals was also recorded (Schwaner, 1979).

Emoia cyanura

This small diurnal skink was caught on the ground and in low vegetation, where it moves rapidly and forages widely. Individuals were disturbed from presumed resting places under rocks and leaf litter at night.

Males.—The 292 specimens have snout-vent lengths of 23-58 mm (Fig. 6). Individuals less than 35 mm had small whitish testes (< 2.0 mm in length). Because there is no apparent break in the testes verses snout-vent length regression (Fig. 7), adult males were estimated from visual inspection of the testes for the presence of enlarged convoluted tubules (Fig. 6). Tubules are only moderately developed in specimens 33-42 mm snout to vent; definite convolutions and vasculation of enlarged testes are found in individuals 38-50 mm and larger. Thus, snout-vent length at maturity in male *E. cyanura* appears to be 38-40 mm. Baker (1947), in a more accurate assessment based on body weight of adult male *E. cyanura* in the New Hebrides, estimated weight at maturity to be 1.5 gms. Among 34 males (with complete tails) weighed prior to preservation during the present study, four were classified as reproductively mature, weighed approximately 1.5 gms (1.5-1.7 gms) and had an average snout-vent length of 42.8 mm (range = 40-43 mm); this is only slightly higher than my estimate for minimal adult maturity based on testes size and condition.

Females.—Of 285 females having snout-vent lengths of 22-56 mm the smallest fecund female (developing ova > 3.0 mm) is 35 mm and the smallest with oviducal eggs, 41 mm (Fig. 6). Thus, the size at sexual maturity of female *E. cyanura* in American Samoa is about 40 mm. Baker (1947) found no oviducal eggs in any female weighing 1.5 gms or less, and estimated the minimum adult weight for female *E. cyanura* in the New Hebrides as 1.6 gms. Of 23 female *E. cyanura* (with complete tails), captured during the present study and weighed prior to preservation, five classified as reproductively active are below 1.6 gms (1.0-1.5 gms) and average 43.5 mm snout to vent. Two individuals weighing 1.6 and 1.7 gms have body lengths of 48 to 46 mm, respectively. This is considerably higher than my estimate of minimum adult size at 40.0 mm based on the size and condition of developing ova. Either females mature at smaller sizes in American Samoa, or there is some discrepancy in equating body size and body weight in these females with the measurements of Baker's (1947) analysis.

Mean clutch size, based on 46 fecund and 46 ovigerous females, and 25 clutches found in the field, is 1.96 (or an almost constant 2

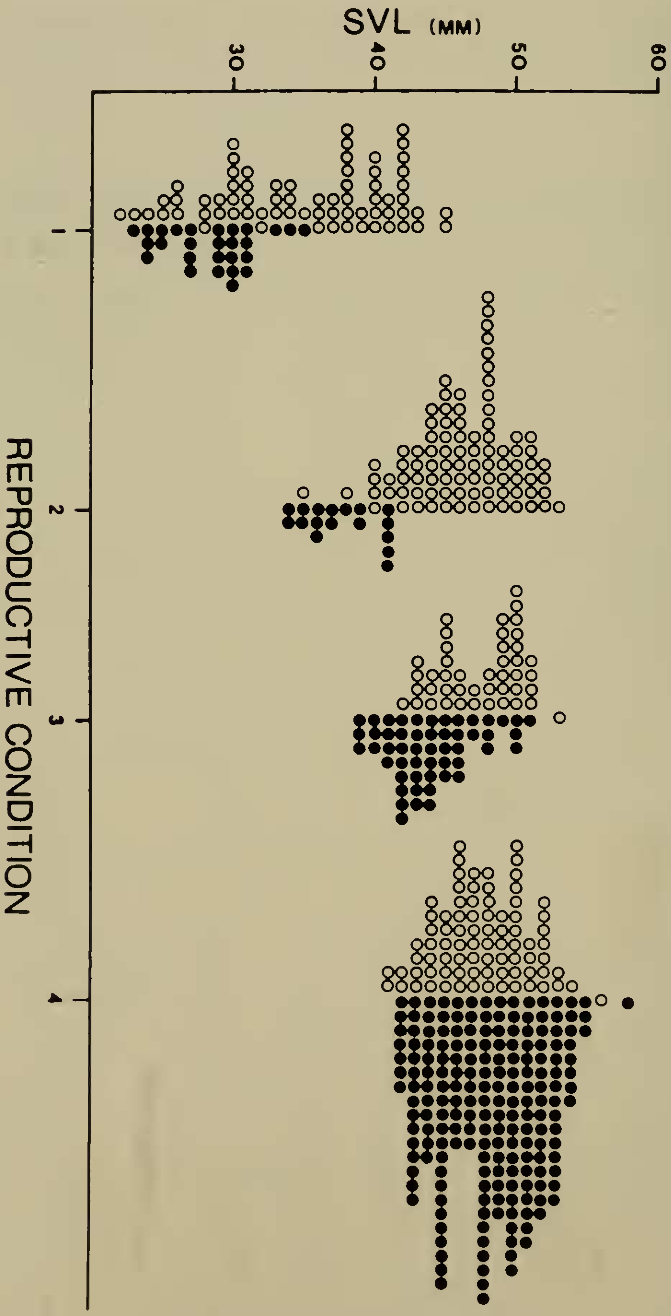

Fig. 6.—Reproductive condition and snout-vent length (in mm) of *Emoia cyanura* from islands of American Samoa. Symbols are as in Fig. 1.

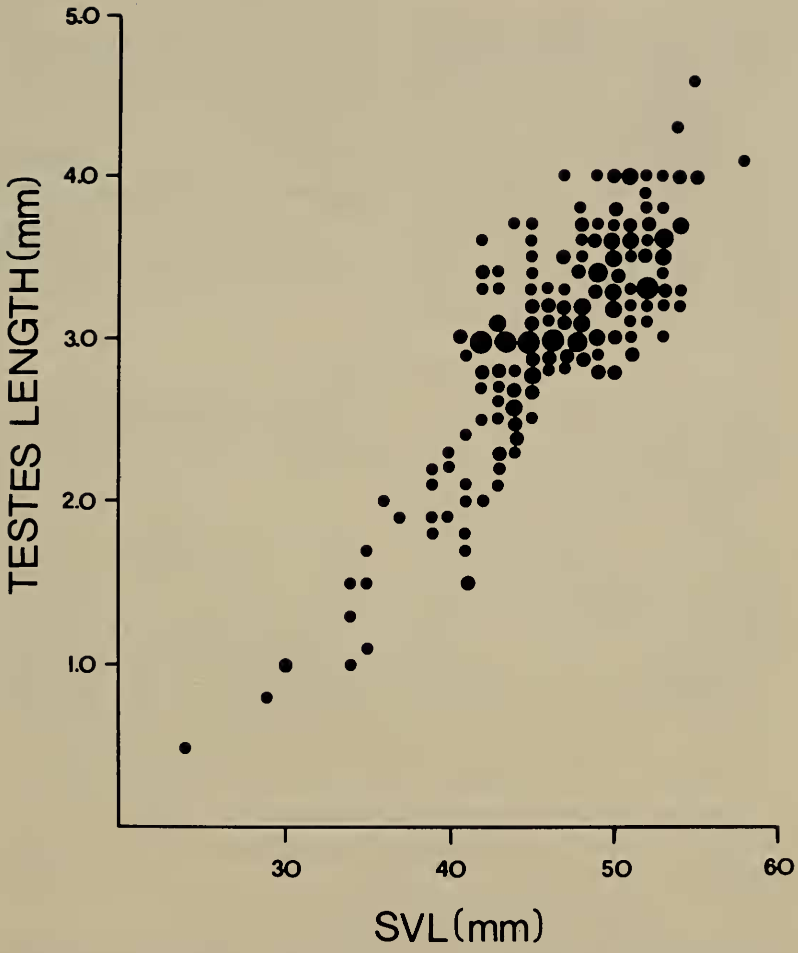

FIG. 7.—Testes length versus snout-vent length (in mm) for male *Emoia cyanura* from American Samoa. Symbols are as in Fig. 2.

eggs per clutch). There is no significant correlation between increasing body size and clutch size (Fig. 3E). Greer (1968), citing Baker (1947), noted that almost always one egg is found in each oviduct of ovigerous females. Similar observations were noted by Hediger (1934) for this species.

The diameters of 39 oviducal eggs measured 9.5-13.2 mm ($\bar{X}$ = 11.2 mm) and closely approximated the length x width of freshly laid eggs ($\bar{X}$ = 12.0 x 7.5 mm, range = 10.2-13.0 X 6.2 X 9.5 mm, n = 18). Incubating eggs of *E. cyanura* swell in size, increasing more in width than in length from partuition to hatching; mean length x width at hatching is 12.6 X 9.5 mm (range = 12.3-12.9 X

9.2-10.1 mm, n = 6). Incubation times were 6-51 days for field collected eggs maintained in the laboratory; however, the upper bound of 40-51 days is probably the usual incubation period. Average hatchling snout-vent length is 22.0 mm (range = 20.0-23.0 mm, n = 45); hatchlings have the adult color pattern.

Emoia cyanura lay eggs in communal nesting sites probably selected for optimal moisture and temperature. Most eggs were taken from under garden rocks; these were usually flat coral plates lying on a sand substrate. The usual number of eggs under the rocks was about 6 to 10; however, one rock covered 70 incubating eggs and many empty egg casings.

Emoia lawesii

This large diurnal skink, was caught on the ground where it forages among coral rubble primarily in littoral forests. None was observed at night.

Males.—The 26 specimens have snout-vent lengths of 77-106 mm (Fig. 8). One male (SVL = 81 mm) has undeveloped testes; however, two smaller individuals (SVL = 77 and 80 mm, respectively) have enlarged testes with convoluted tubules. A conservative estimate of the snout-vent length of reproductively active males is about 85 mm; mature testes lengths are usually above 4.0 mm (Fig. 9). Individuals were collected only during June and July, 1976, and December and January, 1977-1978. Reproductively active males were observed during June, July, December and January.

Females.—Of 38 females having snout-vent lengths of 70-105 mm the smallest fecund female (developing ova > 2.0 mm) is 78 mm and the smallest with oviducal eggs, 88 mm (Fig. 8). Conservatively, reproductive activity of female *E. lawesii* probably begins at snout-vent lengths 85-90 mm.

Mean clutch size, based on 22 fecund and 5 ovigerous females, and 2 laboratory clutches, is 1.8. Most females have two eggs per clutch; two individuals had a single oviducal egg and three others had only one developing ovum each. There is little indication of increasing clutch size with greater body size, but too few females from the lower size range of reproductive maturity were examined (Fig. 3C).

The diameters of 8 oviducal eggs measured 18.0-19.7 mm ($\bar{X}$ = 19.2 mm); at partuition the average egg length x width was 21.3 x 11.8 mm (range = 21.0-21.5 x 11.0-12.5, n = 4). Similar to the other *Emoia* species in this study, the eggs of *E. lawesii* swell during incubation reaching hatching sizes 3.7-4.7 mm longer and wider, respectively, than at partuition. Two eggs laid in the laboratory hatched 72 and 77 days after partuition. This is the longest incubation time for any of the scincid species observed in American

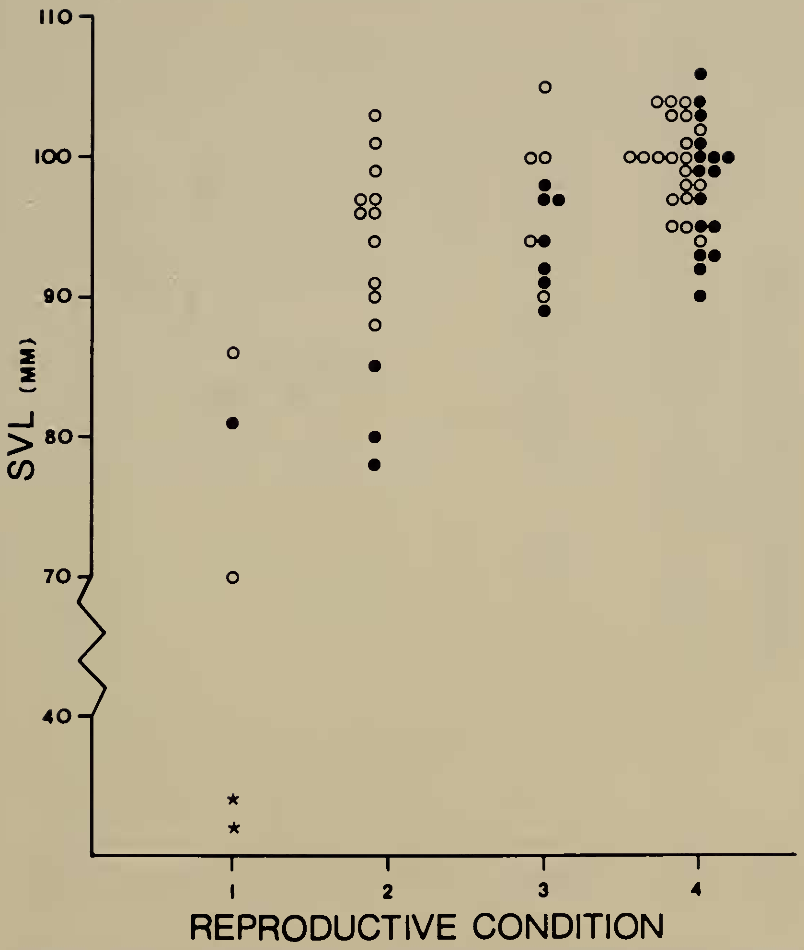

FIG. 8.—Reproductive condition and snout-vent length (in mm) of *Emoia lawesii* from islands of American Samoa. Symbols are as in Figs. 1 and 4.

Samoa. Hatchling color patterns resembled those of adults; snout-vent lengths of two hatchlings were 32.4 mm and 33.4 mm, respectively.

Emoia adspersa

This medium sized diurnal skink was caught on the ground where it was observed to bask and forage. No individuals were observed at night, but three were seen entering and leaving suspected burrows at the bases of trees on Swains Island.

Males.—The 17 specimens examined from Swains, Savaii, Nukunonu and Funafuti islands have snout-vent lengths of 64-84 mm

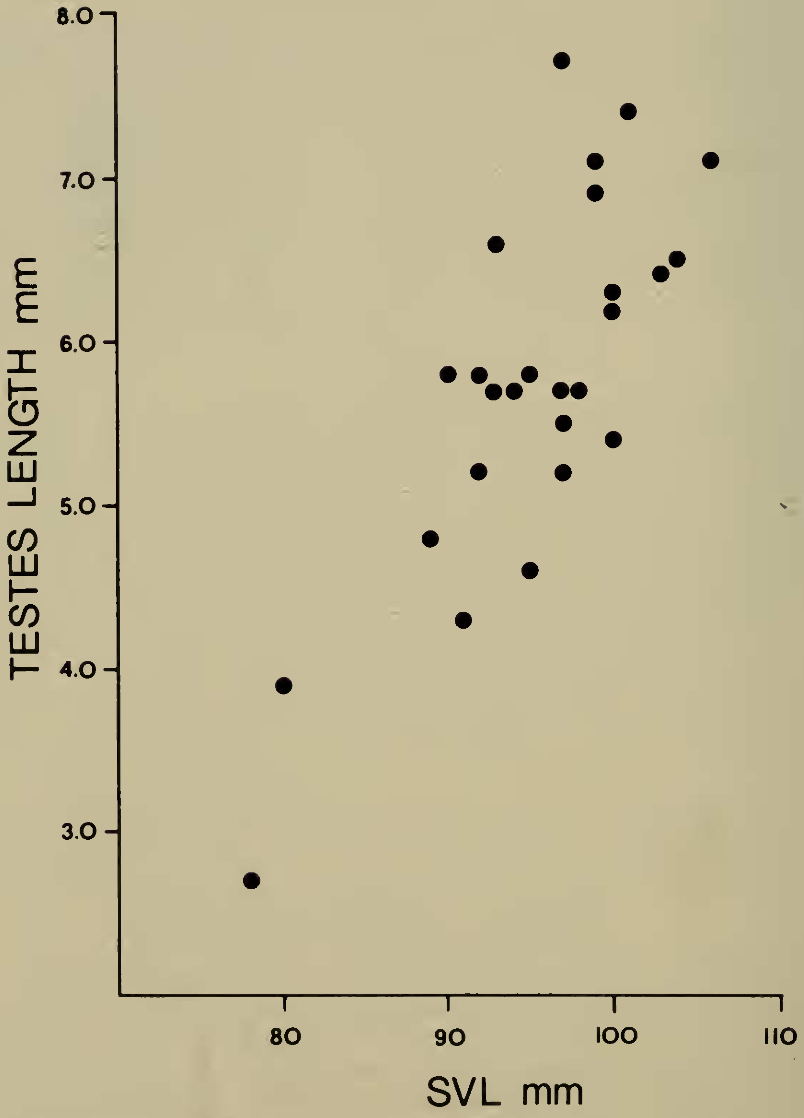

FIG. 9.—Testes length versus snout-vent length (in mm) for male *Emoia lawesii* from American Samoa. Symbols are as in Fig. 2.

(Fig. 10). Only the smallest individual (64 mm) has undeveloped testes; individuals of greater size have testes (with enlarged convoluted tubules) sizes of 3.7-5.5 mm. Conservatively, adult males are probably reproductively active at 65-70 mm snout-vent length. Most individuals (for which dates are available) were taken during the months of April and May, and one each were collected in

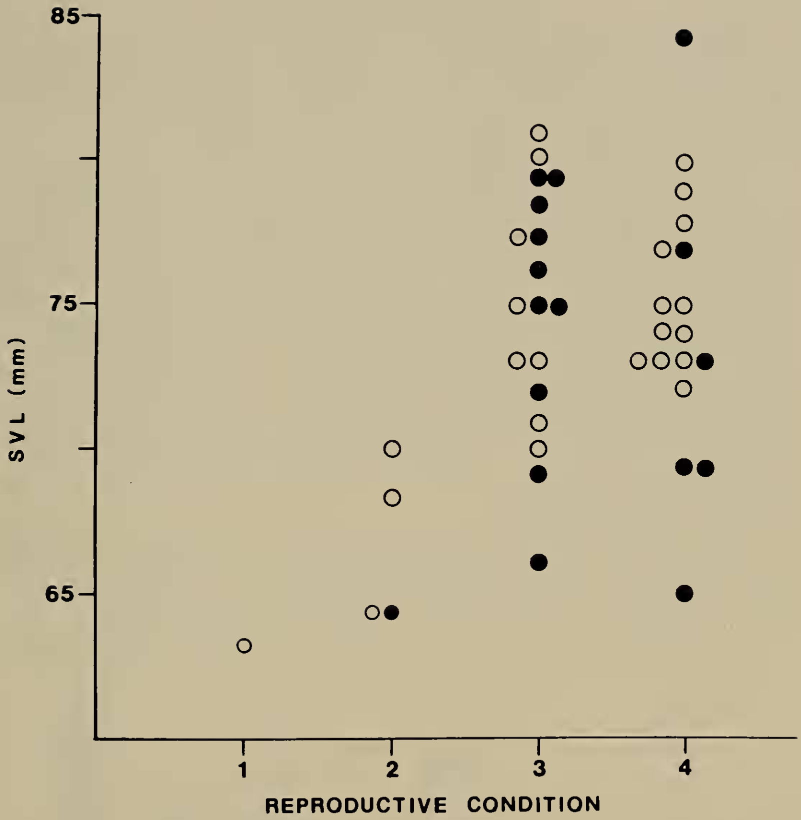

Fig. 10.—Reproductive condition and snout-vent length (in mm) of *Emoia adspersa* from islands of American Samoa, Savaii, Nukunonu, and Funafuti. Symbols are as in Fig. 1.

February and September; all adult specimens have swollen testes with enlarged convoluted tubules and are presumed to have been reproductively active when perserved.

Females.—Of 23 females having snout-vent lengths of 63-81 mm, the smallest fecund female (developing ova > 2.0 mm) is 64 mm and the smallest with oviducal eggs, 70 mm (Fig. 10); thus, conservatively, most females probably are mature at 70 mm.

Mean clutch size, based on 14 fecund and 5 ovigerous females, is 1.9. All but two individuals have two eggs per clutch. Clutch size does not appear to increase with body size (Fig. 3D), but too few females from the lower size range of adults makes this inconclusive. Egg sizes for seven full term oviducal eggs (all with thick leatherly shells) average 16.4 mm (13.4-19.2 mm, n = 7) in length.

Cryptoblepharis boutonii

This small, diurnal skink was caught on coral and lava rocks in littoral strand habitats devoid of vegetation at coastal margins on Ta'u and Olosega islands. None was observed at night, but the species is apparently restricted to the littoral strand.

Males.—The 26 specimens have snout-vent lengths of 25-42 mm (Fig. 11). Individuals less than 37 mm generally have small, whitish testes (< 2.0 mm in length) lacking enlarged convoluted tubules, and are probably immature (Fig. 12). Conservatively, male *C. boutonii* are probably reproductively mature at snout-vent lengths of 38-40 mm and testes sizes of 3.0-4.0 mm in American Samoa.

Females—Of 23 females having snout-vent lengths of 35-48 mm, the smallest fecund female (developing ova > 1.0 mm) is 44 mm and the smallest with oviducal eggs, 43 mm (Fig. 11); one spent female with distended oviducts is 40 mm. The size at sexual maturity for female *C. boutonii* is, therefore, probably at or above 40 mm snout-vent length.

Mean clutch size, based on 12 fecund and 3 ovigerous females, is 1.93; only one individual had one oviducal egg. Thus, the clutch size is probably a constant two eggs in American Samoa.

No eggs were collected from field nests; Haake (1977) states

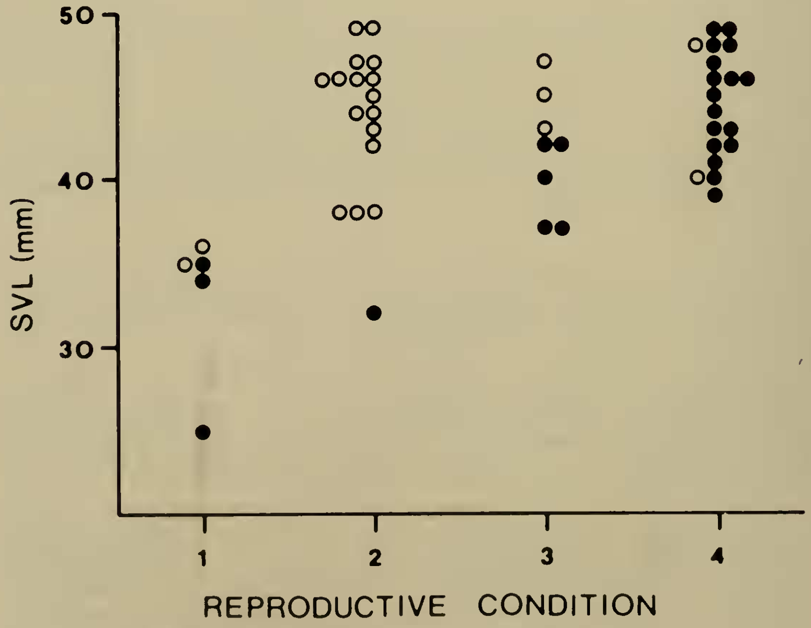

FIG. 11.—Reproductive condition and snout-vent length (in mm) of *Cryptoblepharis boutonii* from islands of American Samoa. Symbols are as in Fig. 1.

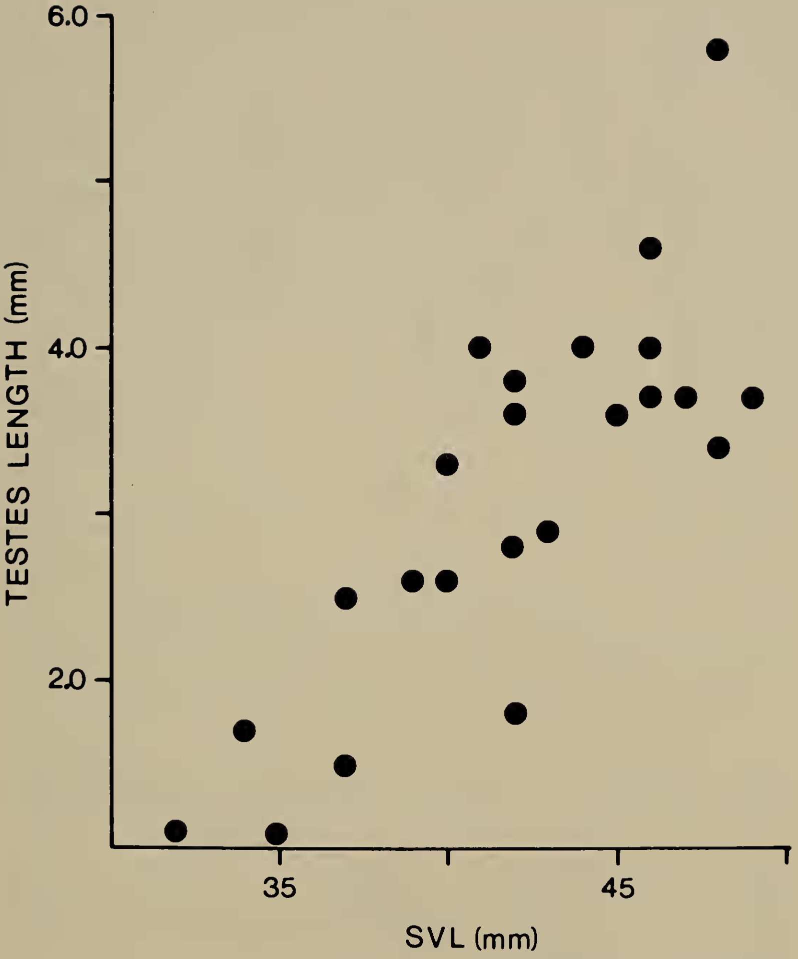

FIG. 12.—Testes length versus snout-vent length (in mm) for male *Cryptoblepharis boutonii* from American Samoa. Symbols are as in Fig. 2.

that the species reproduces "by means of small batches of soft-shelled eggs which are laid in moist sand." The average length of seven oviducal eggs was 10.1 mm (range = 6.9-13.5 mm).

Lipinia noctua

This small, diurnal skink is secretive and almost invariably found under the bark of rotting trees, or in epiphytic vegetation. Individuals were not observed at night.

Males.—The 15 specimens have snout-vent lengths of 25-43 mm (Fig. 13). Individuals less than 35 mm snout-vent length have

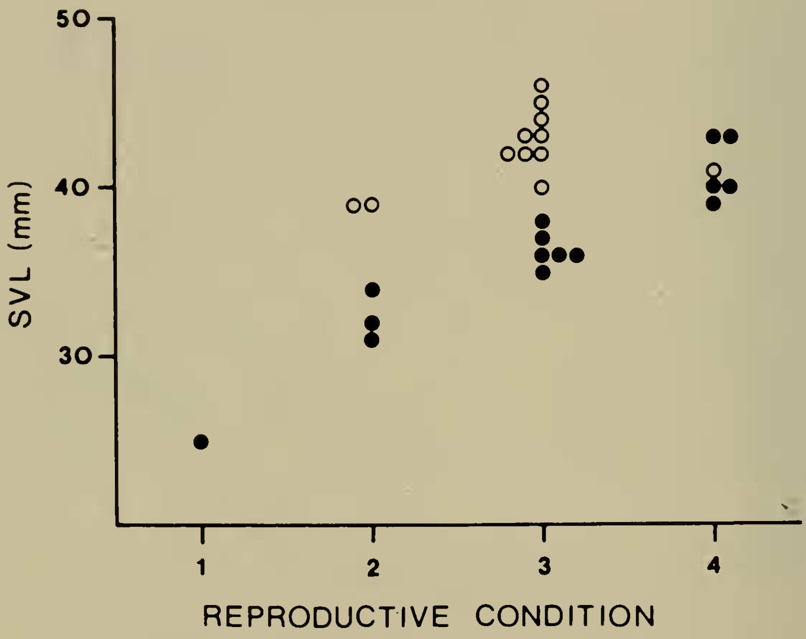

FIG. 13.—Reproductive condition and snout-vent length (in mm) of *Lipinia noctua* from islands of American Samoa. Symbols are as in Fig. 1.

small, undeveloped testes; convoluted tubules in testes > 2.0 mm in length are present in individuals above 35 mm, which is probably the snout-vent length at reproductive maturity (Fig. 14).

Females.—Of 12 females having snout-vent lengths of 39-47 mm the smallest fecund female (developing ova > 1.0 mm) is 39 mm and the smallest ovigerous female, 40 mm; because smaller individuals were not examined, minimal size at reproductive maturity is at least 39 mm (Fig. 13).

Lipinia noctua is viviporous; nine females with developing embryos have two (one in each oviduct), and three females have a single embryo. Fitch (1970) reported Hediger's (1934) observation of one embryo per female in the New Hebrides; Oliver and Shaw (1953) found two embryos in each of six females, and two females with one embryo. Similar results were noted for gravid females from the Marshall, Taumotu, and Marquesas Islands (Fitch, 1970). Gravid females were observed during January, March, June and December in American Samoa; thus reproductive activity is probably year round.

The average diameter of seven embryo masses is 8.9 mm (range = 7.1-10.8 mm). Four full term embryos had an average snout-vent length of 15.5 mm (range = 15.1-16.6 mm).

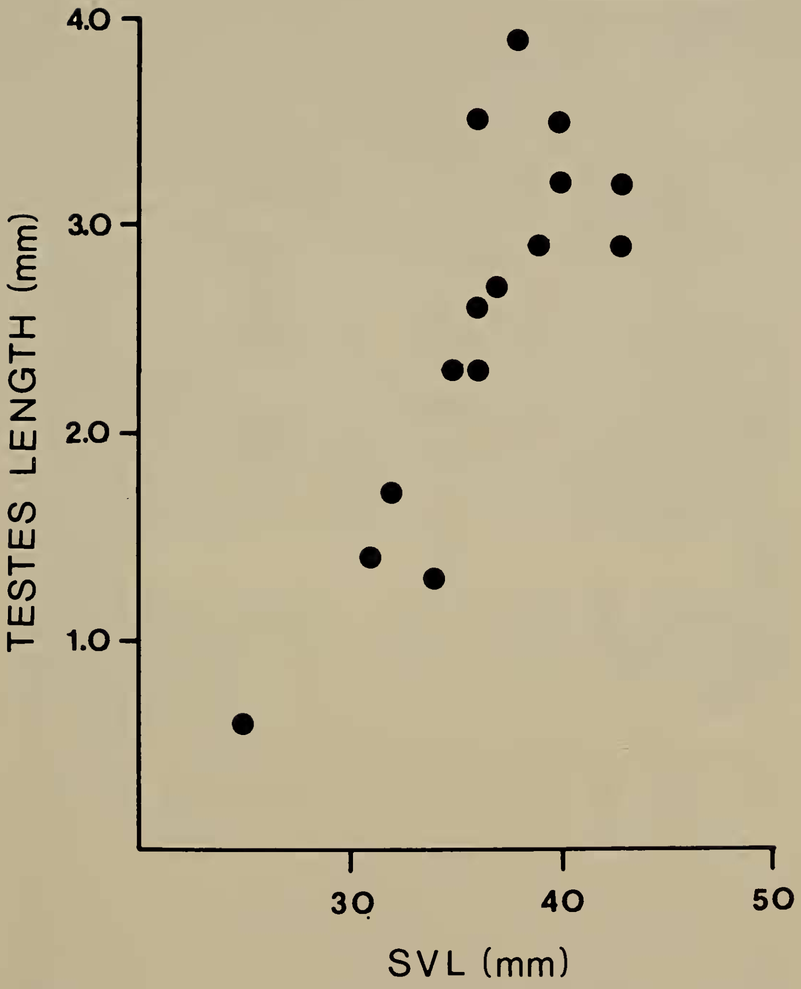

FIG. 14.—Testes length versus snout-vent length (in mm) for male *Lipinia noctua* from American Samoa. Symbols are as in Fig. 2.

Gehyra oceanica

This large, nocturnal gecko was caught on building walls, and on tree trunks in a variety of forested habitats. During the day individuals were disturbed from presumed resting sites under the bark of rotting trees, particularly coconut trees, or from under boards and other debris, and crevices in building walls and roofs.

Males.—The 25 specimens have snout-vent lengths of 36-93 mm (Fig. 15). Reproductively active individuals with enlarged testes and convoluted tubules apparently mature at snout-vent lengths greater than 70 mm in American Samoa; below this size testes are

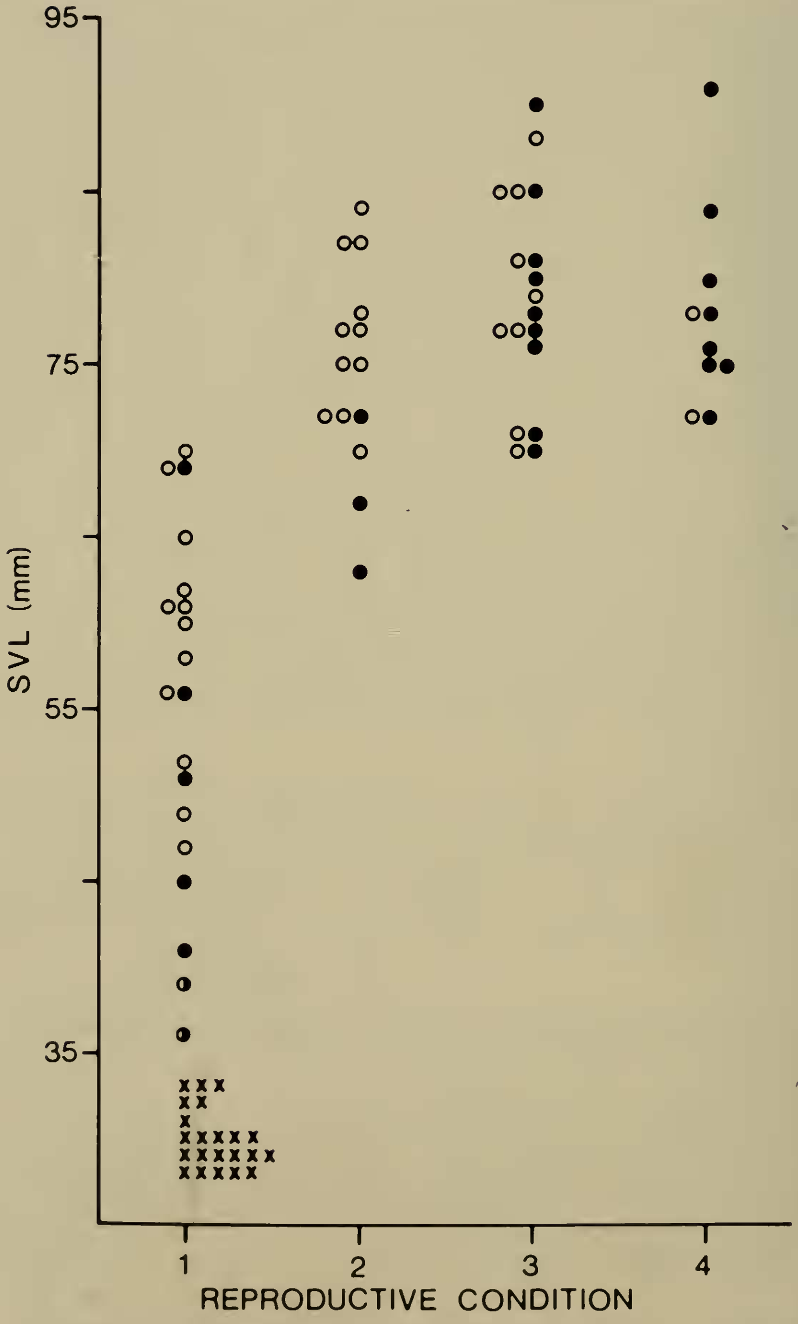

FIG. 15.—Reproductive condition and snout-vent length (in mm) of *Gehyra oceanica* from islands of American Samoa. Symbols are as in Figs. 1 and 4; X's are hatchlings.

small (< 3.0 mm), undifferentiated masses of whitish tissue (Fig. 16). Mature males found during several months of the study are presumably reproductively active year round.

Females.—Of 34 females having snout-vent lengths of 47-67 mm, the smallest fecund female (developing ova > 3.0 mm) and the smallest with oviducal eggs, 70 mm (Fig. 15). Females 70 mm or less have small underdeveloped ova with narrow, undistended oviducts and are apparently immature. Thus, snout-vent lengths of both male and female *G. oceanica* appear to be 70 mm at reproductive maturity.

Mean clutch size, based on 11 fecund and 6 ovigerous females, and 22 clutches found in the field, is 1.96. Most fecund and ovigerous females have two eggs; only two females have a single oviducal egg and one fecund female has four distinctly enlarged ova. A large number of field nests (48%), however, contained a single egg, and a slightly greater percentage (52%) contained two eggs. There is a tendency for females of greater body size to have more than two eggs in a clutch (Fig. 3F), but this trend is not consistent.

Most gekkonid eggs have hard, brittle shells and apparently do not swell during incubation. The diameters of six oviducal eggs measured 7.5-16.5 mm ($\bar{X} = 11.4$ mm); length x width of 25 eggs from field clutches averaged 12.8 x 11.6 mm (range = 12.0-13.6 mm x 11.0-12.5 mm).

Minimum hatching time for *G. oceanica* eggs was 19 days in the laboratory; eggs hatching between 19 and 36 days were usually dark when candled, revealing the eye pigment of developing embryos. Most eggs that hatched beyond 40 days were yellowish or pinkish in color when candled. The longest incubation periods recorded were a rather remarkable 112 and 114 days for two eggs collected on Swains Island in mid-May, 1976. Two eggs from Ta'u Island, taken in January, 1978 took 102 and 109 days to hatch. Brown and Alcala (1957) reported on incubation periods of 70 days for the gekkonid, *Cosymlotus platyurus;* Fitch (1970) cited Loveridge's (1945) note (*sensu* Smith, 1935) indicating a five month incubation period for *Ptychozoan kuklii* in Java; most other gekkonid species for which data are available have incubation times between one and two months. Furthermore, the eggs from American Samoa were kept in dry plastic bags on a shelf in the laboratory and were not considered viable after 3 months, until they unexpectedly hatched. Their apparent resistance to dessication and long incubation times undoubtedly facilitates their transport via rafting among islands.

Hatchlings have snout-vent lengths of 28.0-30.0 mm ($\bar{X} = 29.4$ mm, $n = 19$). Individuals from Swains and Rose islands have a

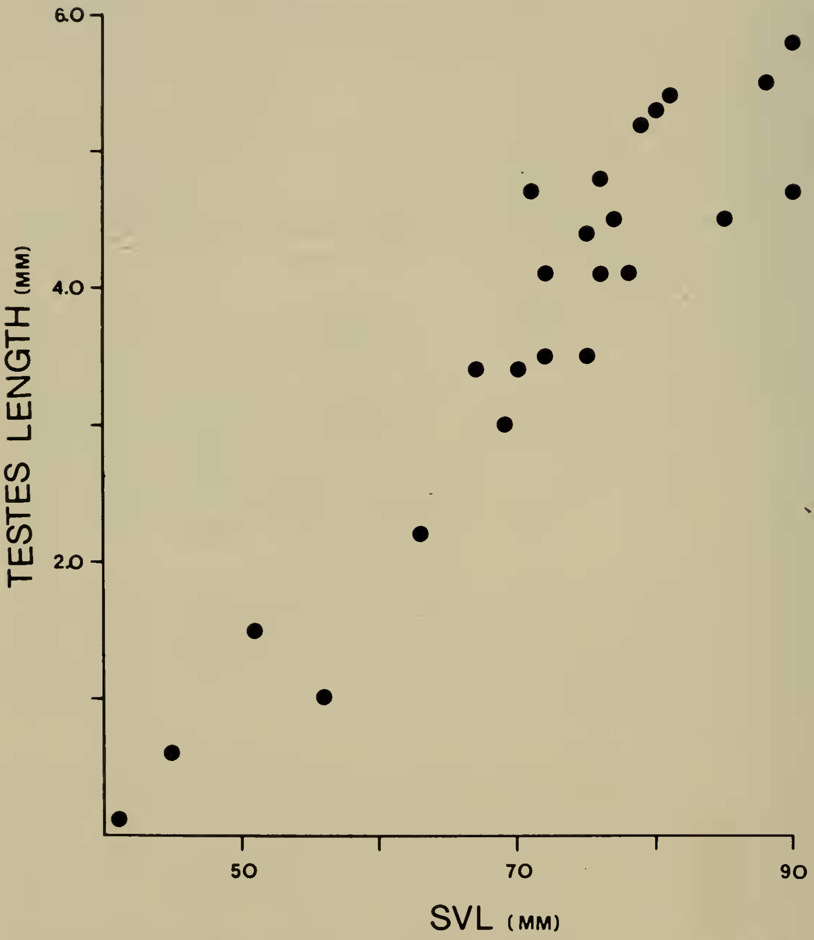

FIG. 16.—Testes length versus snout-vent length (in mm) for male *Gehyra oceanica* from American Samoa. Symbols are as in Fig. 2.

suffusion of rose colored pigment on the underside of the tail, and a faint black midventral line. When alarmed, these hatchlings raise their tails vertically, presumably to display the bright color. Tail autonomy is high in gekkonid species (Pianka and Pianka, 1976), and over 80% of the *G. oceanica* specimens from American Samoa have regenerated tails.

All but one *G. oceanica* egg was found under the bark of rotting coconut stumps, usually near their base; the eggs were in clutches of 1-10, in varying stages of development, indicating communal use of nesting sites. A single egg was found in the tangled roots of a fallen tree.

Hemidactylus frenatus

This medium sized, nocturnal gecko was found exclusively on building walls on Tutuila Island; a small series taken from buildings on Oahu, Hawaii are included with the American Samoan specimens in the following description. No individuals were observed during the day.

Males.—The 18 specimens have snout-vent lengths of 33-60 mm (Fig. 17). Adult males with enlarged testes and convoluted tubules are greater than 40 mm snout-vent length and probably become

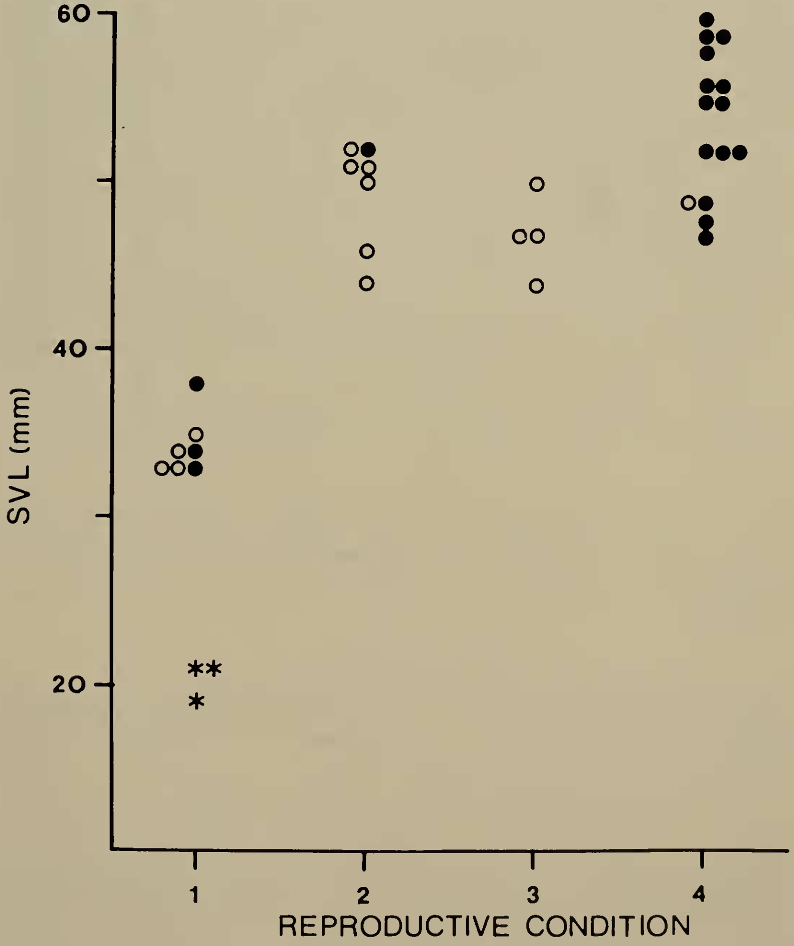

FIG. 17.—Reproductive condition and snout-vent length (in mm) of *Hemidactylus frenatus* from islands of American Samoa (and Hawaii). Symbols are as in Figs. 1 and 4.

reproductively active between 40-50 mm. Most males above 50 mm have testes sizes between 4.0-5.0 mm (Fig. 18). Reproductively active males were found during June and January. Church (1962) observed active reproduction year round in Java; farther north in more temperate areas this pattern became seasonal with peak activity in July and August (Fukada, 1965).

Females.—Of 15 females having snout-vent lengths of 33-52 mm the smallest fecund female (developing ova > 1.0 mm) and the smallest with oviducal eggs are both 43 mm (Fig. 17). Thus, size at reproductive maturity in females in American Samoa (and Hawaii) appears to be greater than 40 mm.

Mean clutch size, based on 5 fecund and 3 ovigerous females, and one field clutch, is 1.9 (or almost a constant 2 per clutch); only one female had a single oviducal egg. Oviducal eggs are only slightly smaller than those freshly laid ($\bar{X} = 7.5$ mm, range $= 6.9$-8.5 mm, $n = 6$). Just prior to hatching the eggs are identical to their size at partuition. Two clutches (four eggs) laid in the laboratory hatched between 77-88 days. These hatching times correspond closely to the "seventy-plus days" reported by Brown and Alcala (1957) for the species in the Philippines Islands. These authors noted that two eggs of *H. frenatus* exposed to sea water for 50 to 168 hrs hatched in 56 days, suggesting that the extent of egg development may not be of significance in determining the effects of sea water. Eggs of American Samoan females were hatched in dry plastic bags. The widespread occurrence of *H. frenatus* throughout the Pacific region and elsewhere is undoubtedly aided by the high resistance of its eggs to a wide range of environmental extremes.

Hatchlings measured 19.0-21.0 mm snout-vent length ($\bar{X} = 20.5$ mm, $n = 5$) and resembled the adults. One clutch of eggs was recovered from the field under a wooden box on the ground near a building wall on Tutuila Island. Hatchlings were not observed in the field.

Peropus mutilatus

This small, nocturnal gecko was found exclusively on darkened buildings not exposed to village lights. It is rare in American Samoa and never observed during the day.

Males.—The 8 specimens have snout-vent lengths of 36-48 mm (Fig. 19). A single individual (31 mm, SVL) is definitely immature (testes size $= 1.2$ mm), and a second individual (36 mm, SVL) has only slightly larger testes (1.4 mm). Five individuals, with enlarged testes and convoluted tubules, range above 40 mm snout-vent length; testes sizes range from 3.0-3.7 mm (Fig. 20). Thus, male *P. mutilatus* in American Samoa probably mature at snout-vent lengths greater than 40 mm. Males taken during July, December and Jan-

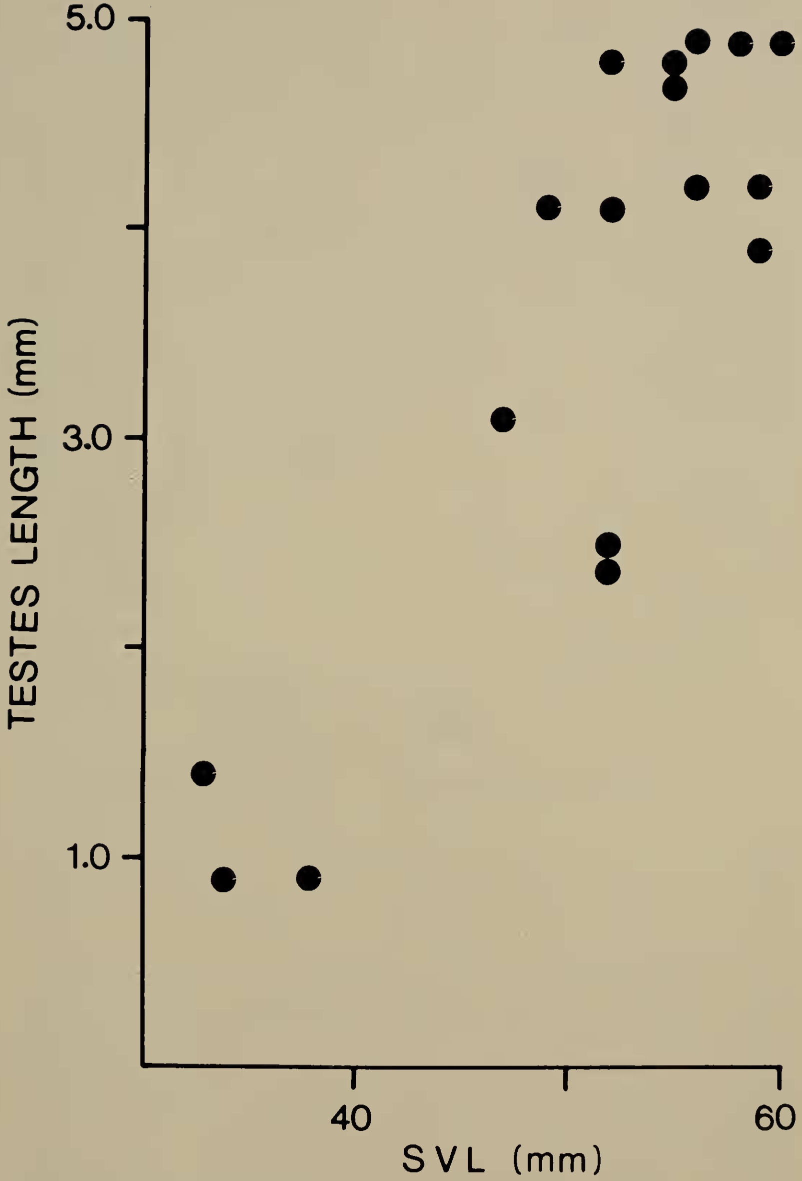

FIG. 18.—Testes length versus snout-vent length (in mm) of male *Hemidactylus frenatus* from American Samoa (and Hawaii). Symbols are as in Fig. 2.

uary were reproductively active. Church (1962) reported year-round breeding for this species in Java.

Females.—Of 12 females having snout-vent lengths of 33-48 mm

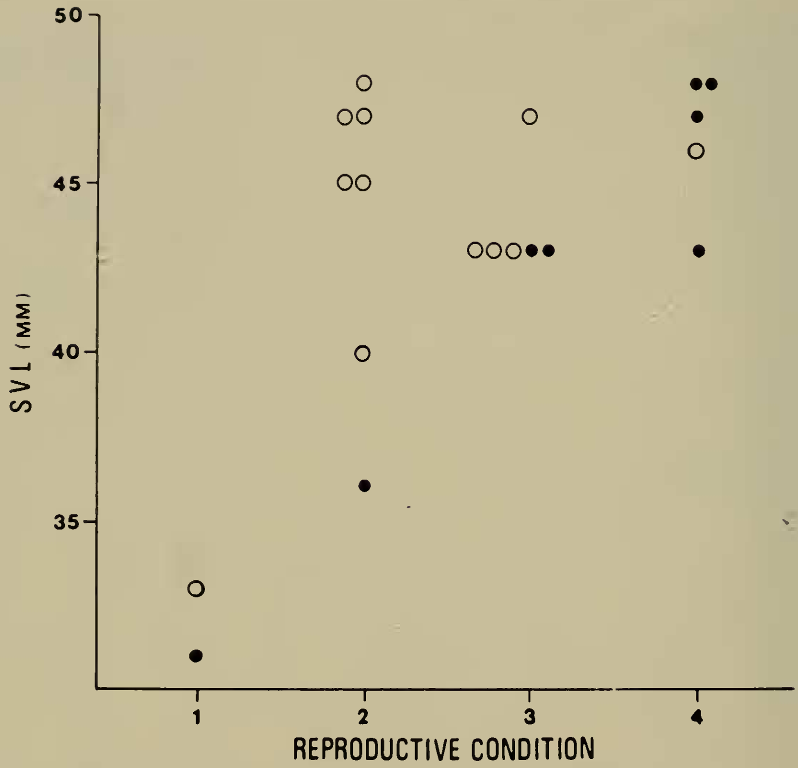

FIG. 19.—Reproductive condition and snout-vent length (in mm) of *Peropus mutilatus* from islands of American Samoa. Symbols are as in Fig. 1.

the smallest fecund female (developing ova > 1.0 mm) is 40 mm and the smallest with oviducal eggs, 43 mm (Fig. 19). Thus, size at reproductive maturity in female *P. mutilatus* from American Samoa is the same as for males, 40 mm.

Mean clutch size, based on 7 fecund and 4 ovigerous females, is 1.8. With the exception of two large females (46 mm and 43 mm, respectively) that probably had laid eggs and were just beginning the development of a second clutch (both were fecund with a single enlarged ovum), all gravid females in American Samoa have two eggs per clutch. Fitch (1970) noted two eggs per clutch for this species in other areas.

Three oviducal eggs measured 6.9-8.1 mm ($\bar{X}$ = 7.5 mm). No eggs were found and hatchlings were not observed in the field.

Cyrtodactylus pelagicus

This medium sized, nocturnal gecko is largely terrestrial. Individuals were usually caught on tree trunks in littoral forest, within

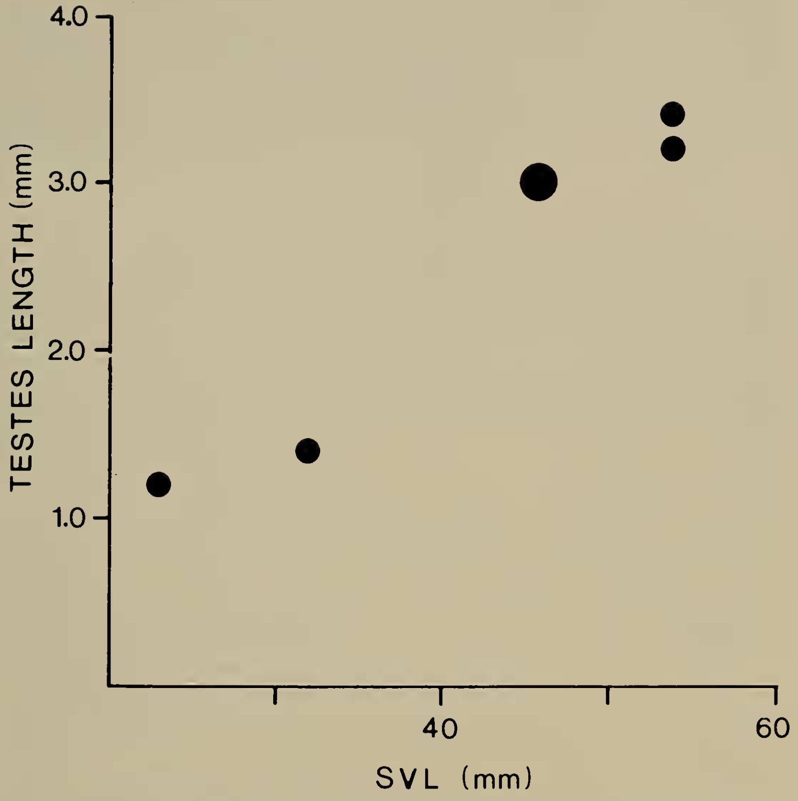

FIG. 20.—Testes length versus snout-vent length (in mm) for male *Peropus mutilatus* from American Samoa. Symbols are as in Fig. 2; large dot represents two individuals.

one meter of the ground; when disturbed the species invariably escaped downward among rocks and litter of the forest floor. Two individuals were captured during the day under debris on the ground in village land. No males were found in any sampled population.

Females.—Of 51 females having snout-vent lengths 23-69 mm the smallest fecund female (developing ova > 1.0 mm) is 50 mm and the smallest ovigerous female, 59 mm (Fig. 21). Thus, reproductive maturity occurs between 50-60 mm snout-vent length in *C. pelagicus* from American Samoa.

Mean clutch size, based on 29 fecund and four ovigerous females, is 1.8; five fecund and two ovigerous females have only one developing ovum each. There is only a slight correlation between body size and clutch size in *C. pelagicus* individuals from American

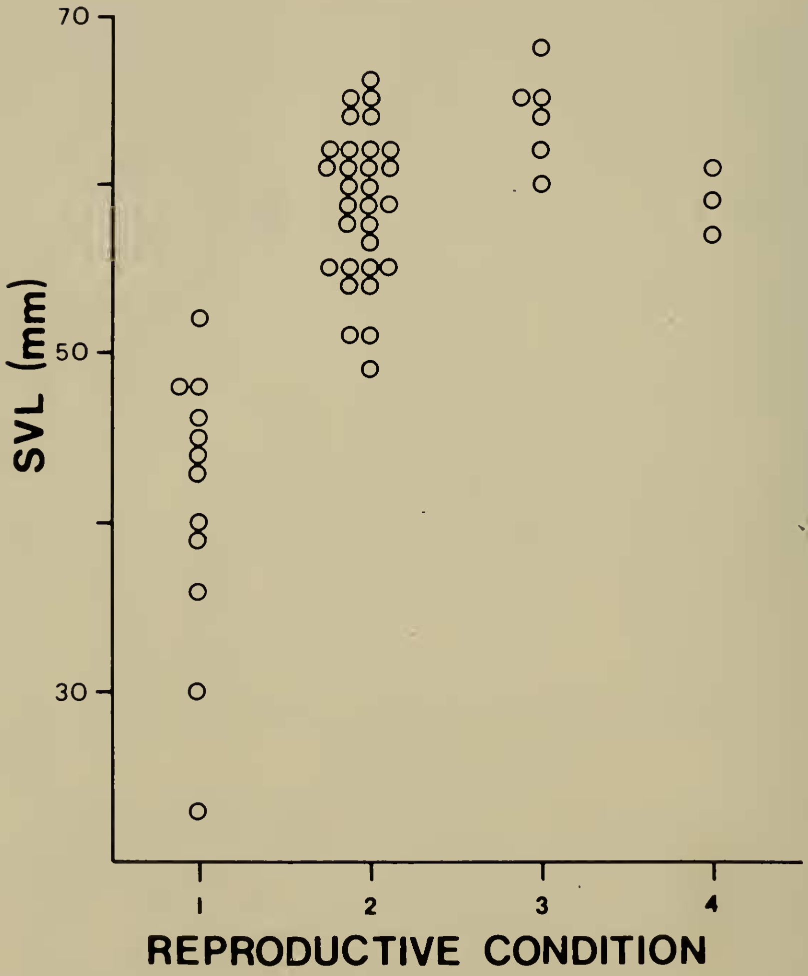

FIG. 21.—Reproductive condition and snout-vent length (in mm) of *Cyrtodactylus pelagicus* from islands of American Samoa. Symbols are as in Fig. 1; this is an all-female population.

Samoa, but more specimens from all size ranges are needed for greater clarity of this point (Fig. 3G).

The diameters of six oviducal eggs measured 9.9-12.0 mm ($\bar{X} =$ 11.3 mm). No field clutches were found, but a single egg laid in a laboratory cage measured 12.2 mm in length. No hatchlings were found in the field.

Two dense populations of *C. pelagicus* were sampled from Ta'u Island, both in littoral forests near the coast. In these habitats few other gekkonid species were found. Most importantly, no males of *C. pelagicus* were collected. Almost all of the females are gravid and there is very little apparent variation in color pattern or measurements of various body parts. One female isolated in the laboratory developed and laid, one egg during a seven month period, but the egg failed to hatch. The lack of males in the collections (taken during July and January) suggests that a parthenogenic population of *C. pelagicus* exists on Ta'u Island.

Lepidodactylus lugubris

This small, nocturnal, abundant gecko was caught in a number of habitats at night, ranging from building walls to village shrubs, forest epiphytes, rotting trees, and the rocky cliffs of coastal strand. Individuals were taken under the bark of trees, in epiphytic vegetation, under debris at the shoreline, in cracks of building walls and roofs, and in crevices between rocks in littoral strand by day. The species is a known parthenogenic form; no males were found in the populations sampled.

Females.—Of 213 females having snout-vent lengths of 20-44 mm the smallest fecund female (developing ova > 1.5 mm) and the smallest ovigerous female are both 35 mm (Fig. 22). Although presumably immature individuals were recorded at higher snout-vent lengths, it seems that female *L. lugubris* from American Samoa mature at 35 mm. Furthermore, the modal snout-vent length for fecund, ovigerous and spent females is 40 mm.

Clutch size, based on 45 fecund and 47 ovigerous females, and 35 field clutches, is essentially a constant 2 eggs. In the field, two eggs in a clutch were observed without error because *L. lugubris* is the only gecko on these islands which lays eggs with shells that adhere to each other upon drying; this was also noted by Cagle (1946) for the species on Tinian Island. These eggs are affixed to the substrate and are difficult to detach without breakage. It is probable that the survival of *L. lugubris* in rocky littoral strands is facilitated by this trait, since affixed eggs may be secured in cracks and crevices of rocks and on cliff overhangs where they escape predation by the numerous crabs along the rocky coastline.

Mean egg size at hatching ($\bar{X} = 8.3 \times 7.1$ mm, range $= 8.0\text{-}9.0 \times 6.8\text{-}7.5$ mm, $n = 3$) is only slightly larger than the mean size of oviducal eggs. The eggs must be extremely resistant to dessication because they were not found in moist (fresh water) areas, but under dead and dying tree bark, rocks exposed to salt spray, and small dry holes in coconut palms. On Rose Island, where *L. lugubris* coexists with *G. oceanica*, eggs of the latter were found under dead tree bark always at the base of the tree, and eggs of the former were always affixed to bark near the top of the tree.

Maximal hatching time in the laboratory was 73 days; two months appears to be the modal incubation period. Oliver and Shaw (1953) reported an incubation time of 92 days, but develop-

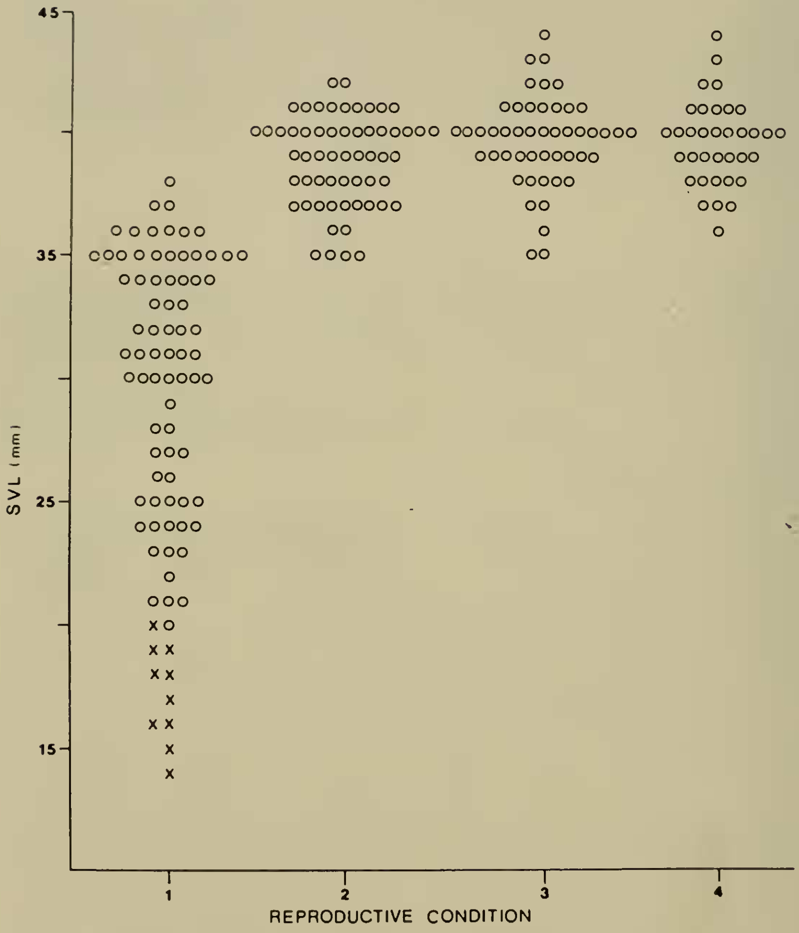

FIG. 22.—Reproductive condition and snout-vent length (in mm) of *Lepidodactylus lugubris* from islands of American Samoa. Symbols are as in Fig. 1; this is an all-female population.

ment was perhaps delayed by cooler than normal incubation temperatures (Fitch, 1970). Mean snout-vent length of hatchlings is 17.1 mm (range = 14.0-20.0 mm, n = 9).

Lepidodactylus lugubris is parthenogenetic (Cuellar and Kluge, 1972); no males were found in American Samoa. The species is distributed from Australia and the Indo-Pacific region, throughout islands of the tropical Pacific Ocean and on mainland Central America and Ecuador (Smith, *et al*, 1961; Fugler, 1966), where it is often the most locally abundant species. Kluge and Cuellar (1972) list the diploid chromosome number as 44. From this they suggested that the mode of parthenogenesis is not due to hybridization with closely related species (or gynogenesis), since no congeners or even closely related genera are found among populations of *L. lugubris,* wherever it is found. Undoubtedly the wide range of *L. lugubris* both in geography and habitat distributions in American Samoa (Schwaner, 1979), is facilitated by its unique combination of reproductive habits.

DISCUSSION

Patterns in Monthly Reproductive Activity

To demonstrate the apparent constancy of the American Samoan islands with respect to annual patterns in temperature and rainfall, Colwell's (1974) method was used in an analysis of predictability, constancy and contingency for monthly averages of precipitation and temperatures taken from published weather records for 17 consecutive years (U.S. Bureau of Standards, 1960-1976). These data are cast into the matrices of Tables 1 and 2, respectively, for predictability analyses, along with the computed proportions of constancy and contingency contributing to predictability. Rainfall (Table 1) is highest during December to April (the so called "rainy season"); drier months are from May to December, having lows in August and September. The pattern is not marked, however, and its predictability is only 54%. Constancy of the pattern is high however (48%) in contrast to the contingency factor (6%); the former factor contributes 88% to the predictability of the pattern (as opposed to only 12% for contingency). Therefore, whereas the pattern

TABLE 1.—Predictability, constancy and contingency matrix for mean monthly distribution of precipitation on Tutuila Island, American Samoa, for the years 1960-1976. Rainfall is divided into logarithmically increasing classes, with the upper bound at > 64.00 cm.

Amount monthly rainfall (cm)	Months											
	S	O	N	D	J	F	M	A	M	J	J	A
0.00												
1.00												
2.00	1										1	1
4.00	2	1	1								2	
8.00	7	2			1			1		3	4	5
16.00	5	4	7	5	5	6	8	2	9	8	6	8
32.00	1	9	9	8	9	9	6	12	7	6	3	3
64.00	1	1		4	2	1	2	2	1			
> 64.00						1	1					

Predictability = .54
Constancy = .48
Constancy/Predictability = .88
Contingency = .06
Contingency/Predictability = .12

TABLE 2.—Predictability, constancy and contingency matrix for mean monthly temperature distributions on Tutuila Island, American Samoa, for the years 1960-1976. Temperature is divided into logarithmically increasing classes, with the upper bound at > 28.20°C.

Mean monthly temperature (°C)	Months											
	S	O	N	D	J	F	M	A	M	J	J	A
25.00												
25.05												
25.10												
25.20												
25.40												
25.80	8	4	1	2	1	2		1	3	4	10	13
26.60	9	13	16	12	12	9	13	11	14	13	7	4
28.20				3	4	6	4	5				
> 28.20												

Predictability = .78
Constancy = .61
Constancy/Predictability = .78
Contingency = .17
Contingency/Predictability = .22

is highly constant (p < .001) and thus predictable (p < .001), it is not due to contingency (or seasonality, p > .95).

Mean monthly temperatures (Table 2) are highly predictable (78%, p < .001). Constancy contributes a highly significant 78% (p < .001) to the predictability of temperature, but contingency accounts for a nonsignificant 22% (p > .5) of the pattern. Mean monthly temperatures vary only 1.3°C throughout the year. Thus, there is no statistical basis for recognizing seasonality in temperature or precipitation on American Samoan islands, and the climate is highly predictable by its constancy (at least during the years for which measurements were analyzed).

Monthly collections of individuals of *Emoia nigra, E. samoense* and *E. cyanura* were sufficiently large (although unevenly distributed) to detect patterns in reproductive activity. I defined three categories of adult female reproductive status: (1) Ovigerous females contain oviducal eggs; (2) fecund females are of minimal adult body size (as estimated above) and contain enlarged ova (> 3.0 mm in diameter for *E. cyanura*, > 5.0 mm for *E. nigra*, and > 4.0 mm for *E. samoense*); and (3) non-fecund females have minimal adult body sizes and ova sizes less than those for fecund individuals. Reproductively active females are both ovigerous and fecund (Tables 3 and 4).

Maximal reproductive activity for *Emoia cyanura* was highest from November to April and lowest from May to October (Fig. 23). Reproductively active females were found in most months of the year, however, and were never below 25% frequency. When the

TABLE 3.—Mean monthly data for climatic parameters and monthly percents of *Emoia nigra*, *E. samoense* and *E. cyanura* females in reproductive condition from islands of American Samoa. Climatic data are from Amerson, *et al.* (1978, unpublished) for the years 1956 to 1976.

Climatic parameters[1] and lizard species	Months J	F	M	A	M	J	J	A	S	O	N	D
MMAT	27.3	27.2	27.3	27.2	26.8	26.6	26.2	26.0	26.4	26.6	27.0	27.2
MMRN	325	322	292	312	244	216	178	182	165	302	269	360
MMSC	8.1	8.3	7.7	7.8	7.3	6.8	6.8	6.5	6.4	7.4	7.6	7.9
MRHA	76	76	76	76	76	77	75	74	73	76	76	75
MRHN	89	90	91	90	89	86	84	85	85	85	86	86
MMWS	8.0	6.5	6.5	7.5	8.0	11.0	11.5	11.5	10.5	11.0	9.5	8.0
DURD	762	744	726	708	690	672	690	708	726	744	762	780
E. nigra	25	–	28	40	67	41	25	–	–	40	0	20
E. samoense	15	–	43	50	–	–	43	–	–	50	66	15
E. cyanura	49	–	80	33	36	26	39	–	–	25	–	58

[1] MMAT = Mean monthly air temperature (°C).

MMRN = Mean monthly rainfall (inches).

MMSC = Mean monthly sky cover.

MRHA = Mean monthly relative humidity (1300 hrs).

MRHN = Mean monthly relative humidity (0100 hrs).

MMWS = Mean monthly wind speed (mph).

DURD = Duration of daylight (monthly) in minutes.

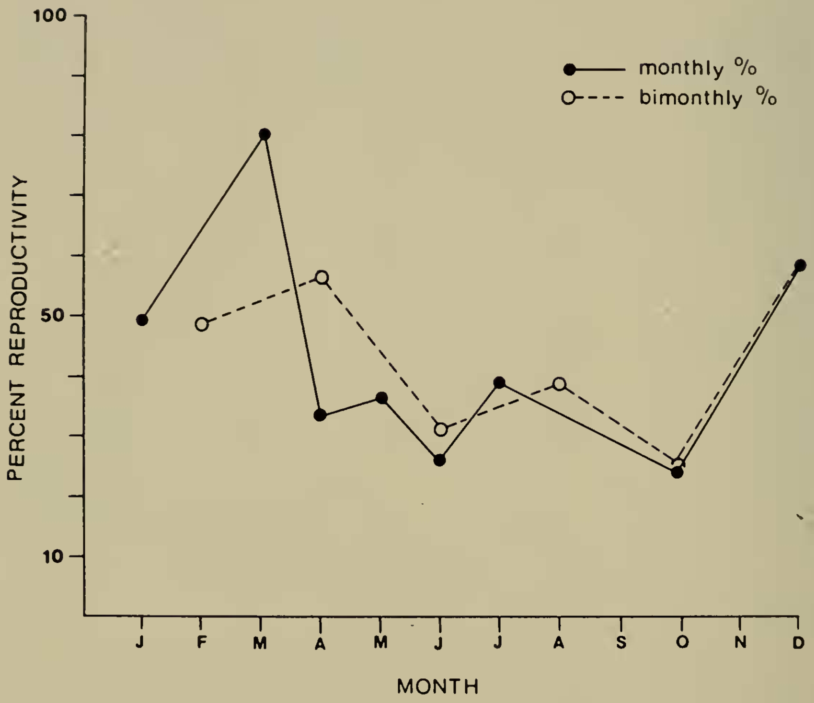

FIG. 23.—Monthly and bimonthly percent of reproductively active (ovigerous and fecund) females of *Emoia cyanura* from islands of American Samoa.

various stages of the reproductive cycle (ovigerous, fecund and spent females, and hatchlings) are considered separately (Fig. 24), the monthly percentages of spent females (relative to the total number of reproductive stages) is inversely proportional to similarly computed frequencies of hatchlings, with maximal divergence in December, March, and June. If eggs are laid in January (as indicated by the small peak in frequency of spent females) and hatch within about two months (as suggested by incubation times in laboratory clutches), hatchlings would emerge in March and April, as illustrated by the peak in hatchling frequencies during those months. Percentages of fecund and ovigerous females increase from October to December and January and decline with spent frequencies toward March. Large numbers of field clutches were found in February and March, 1976 (and again in June, 1976). Percentages of fecund females increase slightly from a low in March to a peak in May, and frequencies of spent females peak a month later, while the former drops to its lowest point (14%) during the months sampled. Hatchling percentages also reach a low (10%) in June.

Monthly mean diameters of developing ova (numbers in paren-

TABLE 4.—Monthly numbers of ovigerous, fecund, nonfecund and spent adult females, hatchlings and mean ova sizes of fecund (and nonfecund) females for three species of scincid lizards from American Samoa. Dashes (–) indicate no data were taken.

	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
Emoia nigra												
Ovigerous	8	–	2	3	0	6	1	–	–	2	0	7
Fecund	5	–	0	3	4	3	3	–	–	0	–	2
Nonfecund	39	–	5	9	2	13	12	–	–	3	1	35
Spent	21	–	0	2	0	1	4	–	–	0	0	26
Hatchlings	1	–	1	6	0	3	1	–	–	0	0	0
Mean ova size	3.6	–	3.6	5.9	7.6	4.0	5.7	–	–	–	–	4.3
E. cyanura												
Ovigerous	19	–	1	7	2	4	1	–	–	0	–	6
Fecund	18	–	3	6	7	4	4	–	–	1	–	2
Nonfecund	38	–	1	26	16	23	8	–	–	3	–	6
Spent	27	–	1	16	14	34	7	–	–	4	–	3
Hatchlings	2	–	10	21	10	4	0	–	–	0	–	0
Mean ova size	4.2	–	3.9	3.0	4.4	4.8	3.1	–	–	3.1	–	3.1
E. samoense												
Ovigerous	2	–	2	1	0	–	2	–	0	1	1	1
Fecund	1	–	1	0	0	–	1	–	0	0	1	2
Nonfecund	17	–	4	1	3	–	4	–	1	1	1	18
Spent	18	–	1	0	1	–	1	–	1	1	0	4
Hatchlings	1	–	0	1	0	–	11	–	0	0	0	1
Mean ova size	3.5	–	3.3	3.2	2.6	–	2.7	–	–	–	–	2.5

thesis above fecund frequencies in Fig. 24) appear to increase in size from December, peaking in January, and then decreasing in average size from January to April, just at the time when ovigerous and spent females of *E. cyanura* also decline in frequency. Ova sizes increase again in April and May, and decline in June, the same month during which spent females reach peak frequencies.

The failure of ovigerous frequencies to increase and peak just prior to the high peak of spent females in May and June is inconsistent with patterns seen from October to December. This may be a result of low sample sizes for those months; however the overall unevenness of samplings during all months of the study strains the credibility of any stronger conclusion. The data do seem to follow a consistent pattern which appears to result in two peaks of egg production, one from December to January, and another in June and July; critical data from August and September are entirely lacking, however, and greater sample sizes for each month are obviously needed.

Maximal reproductive activity for *Emoia nigra* seems to peak

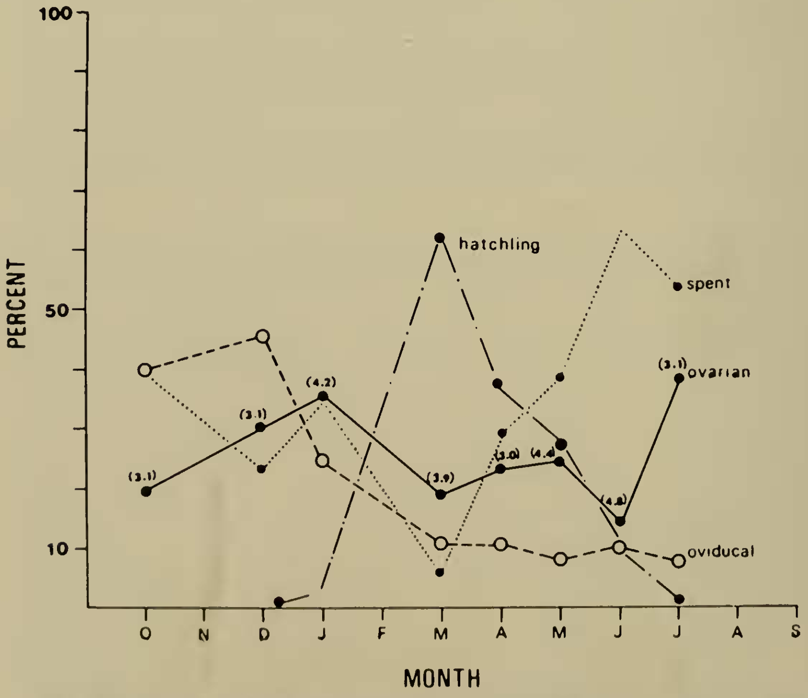

FIG. 24.—Monthly percent of the total counts for hatchlings, spent females, fecund females (ovarian) and ovigerous (oviducal) females of *Emoia cyanura* from islands of American Samoa. Numbers in parentheses above fecund females are mean ova sizes for that month.

from March to June, and again, slightly, in September and October (Fig. 25); these peaks although broadly overlapping those of *E. cyanura,* occur somewhat later than for the smaller species. Reproductively active females of *E. nigra* were found during each sampled month, reaching their lowest frequency (20%) in December.

Spent females are at highest percentages in December, declining to zero percent in March (Fig. 26). Frequency of hatchlings, however, increases from December to a peak in April, approximately three months later. Obviously, if eggs are deposited in December and January, and require from two to three months to hatch as previously suggested, hatchlings should be most abundant in March and April.

Mean ovum sizes (in parenthesis above fecund frequencies in Fig. 26) show enlarging ova from December to January, decreasing in mean size in March and then markedly increasing again from April to May. These patterns generally precede and parallel those for increasing and decreasing frequencies of ovigerous females of *E. nigra.* Apparently eggs mature in December and January, are deposited, and hatch in May and April; a second developmental period occurs from March to May and eggs are again deposited

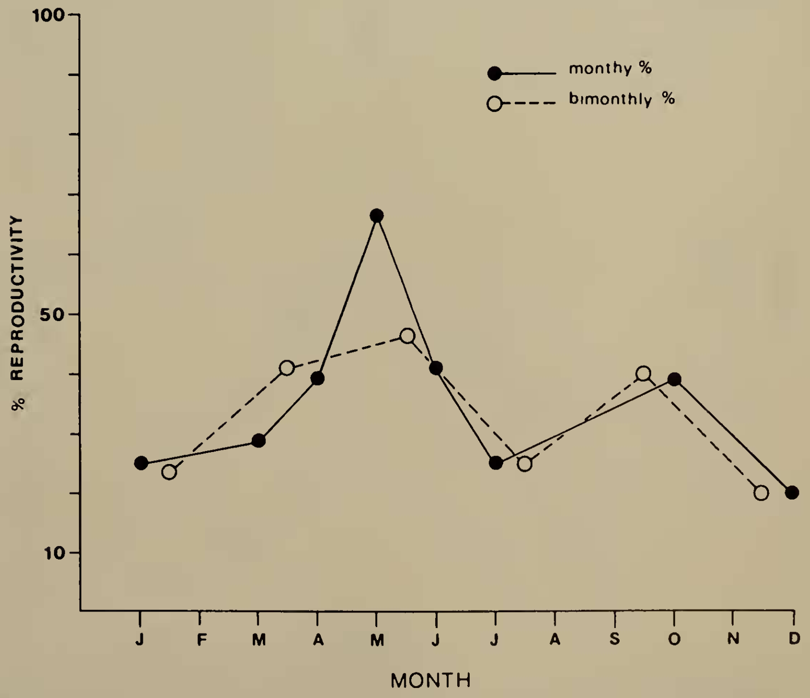

FIG. 25.—Monthly and bimonthly percent of reproductively active (ovigerous and fecund) females of *Emoia nigra* from islands of American Samoa.

(although perhaps not necessarily from the same females) in June and July.

Reproductive activity in *Emoia samoense* exhibits much greater peaks and valleys than the species analyzed above (Fig. 27). While it may also be due to low sample sizes, assuming it is not, the pattern is markedly different. Maximal activity (using the bimonthly data) peaks in March and April, and again, more steeply, in December. Reproductively active females were not found in May (and no specimens were collected during June due to scheduled trips during that month to islands where *E. samoense* was not present).

Frequencies of spent females are highest from September to January and lowest from April to June (Fig. 28); eggs deposited in January presumably incubate for one to two months and would be expected to hatch in late February or early July. Hatchlings were found from December to July, and were most abundant in April. Percentages of ovigerous females drop sharply from October to January, but ova sizes (numbers in parenthesis above fecund frequencies, Fig. 28) increase from December to January and main-

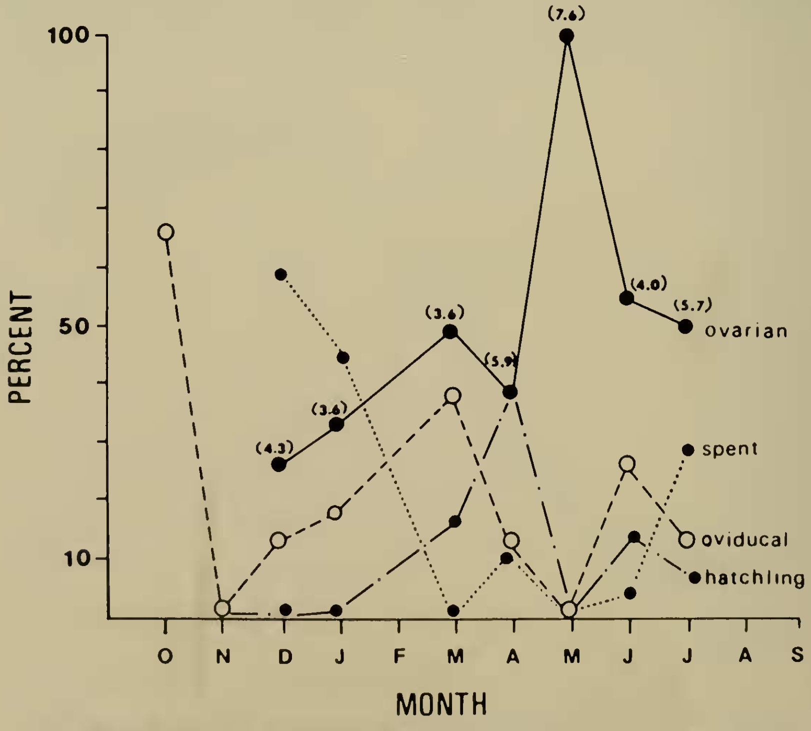

Fig. 26.—Monthly percent of the total counts for hatchlings, spent females, fecund females (ovarian) and ovigerous (oviducal) females of *Emoia nigra* from islands of American Samoa. Numbers in parentheses above fecund females are mean ova sizes for that month.

tain constant sizes (3.2 to 3.5 mm) through April. Ovigerous female frequencies increase in parallel with ova sizes from December to a peak in April. Although peak egg deposition clearly contrasts with low frequencies of ovigerous females, the patterns are not as well defined as those found for *E. nigra* and *E. cyanura.* The prolonged increase in ovigerous female frequencies from January to April, and the maintenance of a relatively high ovum size during the same time period, suggests that *E. samoense* may hold developing eggs longer and deposit them more slowly than either *E. nigra* or *E. cyanura.*

Correlations

Mean monthly climatic variables and monthly percents of reproductively active females of *E. nigra, E. samoense* and *E. cyanura* (Table 3) were analyzed to derive Pearson product-moment correlation coefficients (r's). As expected, certain climatic variables are highly correlated (Table 5). Mean monthly air temperature is positively correlated with all but mean monthly wind speed ($r = 0.97$, $p < .001$), and significantly with mean monthly rainfall ($r = .82$, $p < .01$), mean monthly sky cover ($r = .94$, $p < .001$), and mean

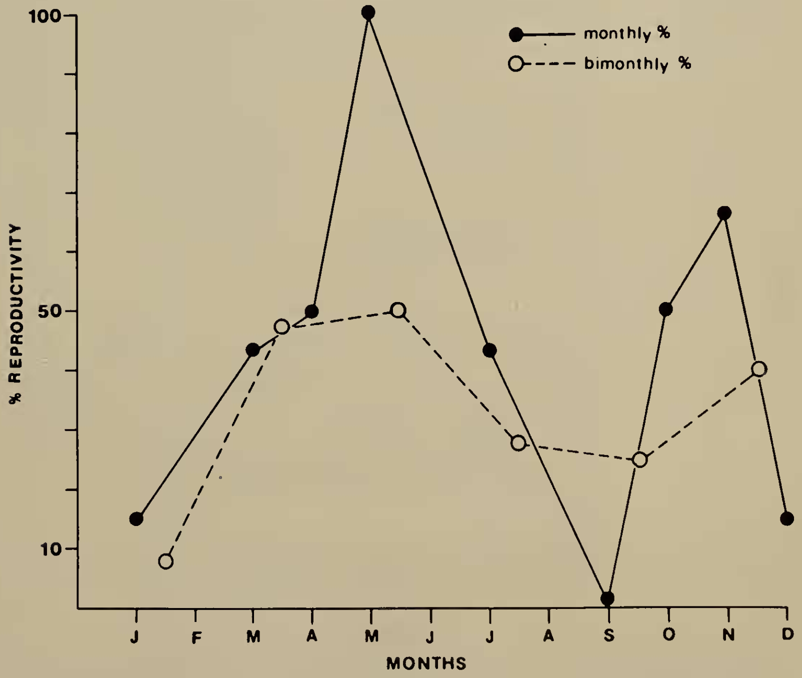

FIG. 27.—Monthly and bimonthly percent of reproductively active (ovigerous and fecund) females of *Emoia samoense* from islands of American Samoa.

monthly relative humidity (0100 hrs) ($r = .83$, $p < .01$). Mean monthly relative humidity (0100 hrs) is also negatively correlated with mean monthly wind speed ($r = -.64$, $p < .05$), and significantly with mean monthly sky cover ($r = .91$, $p < .001$) and duration of daylight ($r = .82$, $p < .01$). Mean monthly sky cover is negatively correlated with mean monthly wind speed (−.80, $p < .01$), but positively with other variables and significantly with mean monthly relative humidity (0100 hrs) ($r = .66$, $p < .05$) and duration of daylight ($r = .70$, $p < .05$). Mean monthly relative humidity (1300 hrs) is slightly negatively correlated only with mean monthly wind speed, but positively with mean monthly relative humidity (0100 hrs) ($r = .67$, $p < .05$). Mean monthly wind speed is negatively correlated with all variables and significantly with those mentioned above.

These correlations characterize the maritime tropical climate of American Samoa in the Southern Hemisphere where there is only slight seasonality. Slight increases in temperature and rainfall during the months of November to April are accompanied by greater

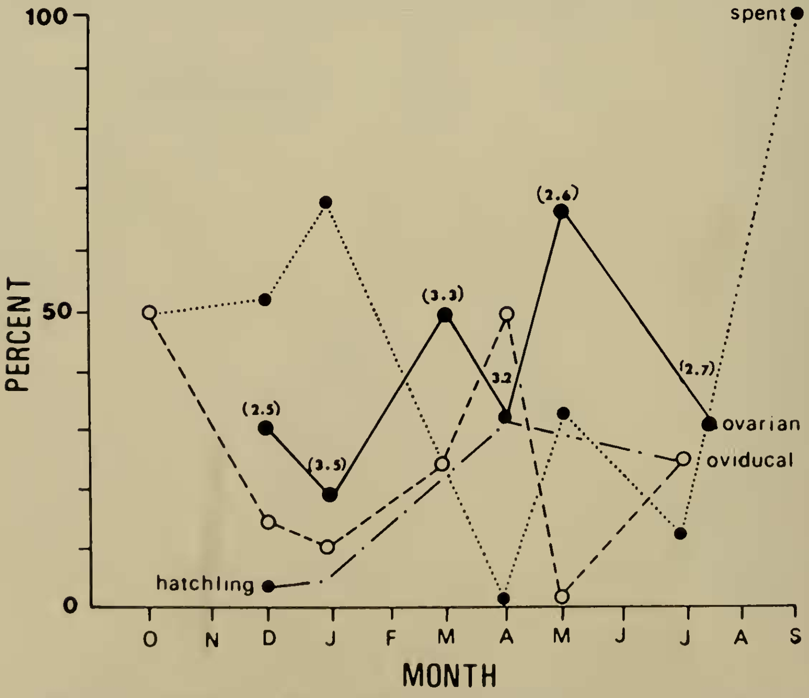

FIG. 28.—Monthly percent of the total counts for hatchlings, spent females, fecund females (ovarian) and ovigerous (oviducal) females of *Emoia samoense* from islands of American Samoa. Numbers in parentheses above fecund females are mean ova sizes for that month.

Table 5.—Correlations of climatic variables and percent reproductive activity of three lizard species from American Samoa. Climatic data averaged from monthly summaries between 1956 to 1976. Abbreviations are as in Table 3; CYAN = *Emoia cyanura,* NIGR = *E. nigra,* SAMO = *E. samoense.*

	MMAT	MMRN	MMSC	MRHA	MRHN	MMWS	DURD	CYAN	NIGR	SAMO
MMAT	1.00									
MMRN	0.82[b]	1.00								
MMSC	0.94[c]	0.91[c]	1.00							
MRHA	0.45	0.33	0.44	1.00						
MRHN	0.83[b]	0.44	0.66[a]	0.67[a]	1.00					
MMWS	–0.94[c]	–0.64[a]	–0.80[b]	–0.38	–0.90[c]	1.00				
DURD	0.54	0.82[b]	0.70[a]	–0.00	0.02	–0.30	1.00			
CYAN	0.55	0.22	0.34	–0.04	0.52	–0.69	0.24	1.00		
NIGR	–0.11	0.01	–0.08	0.66[a]	0.14	0.14	–0.36	–0.60	1.00	
SAMO	–0.44	–0.48	–0.56	0.32	–0.00	0.29	–0.76[a]	–0.36	0.78	1.00

[a] $p < .05$

[b] $p < .01$

[c] $p < .001$

sky cover, relative humidity, duration of daylight, and significantly reduced wind speeds. The Southeast Trades blow stronger from June to October when temperature and rainfall are reduced, accompanied by generally shorter days, reduced sky cover, and lower relative humidity.

The only significant correlations for *Emoia nigra, E. samoense* and *E. cyanura* with climatic variables (Table 5) are a positive one for *E. nigra* and mean monthly relative humidity (0100 hrs) ($r = .66$, $p < .05$), and two negative correlations, *E. samoense* and duration of daylight ($r = -.76$, $p < .05$), and *E. cyanura* and mean monthly wind speed ($r = -.69$, $p < .05$). There are no significant correlations among the reproductively active periods of the three *Emoia* species, but the correlation between *E. nigra* and *E. samoense* is moderately high and positive ($r = .78$, $.05 < p < .1$). Most interesting is the moderately high, but negative correlation between the reproductive activities of *E. cyanura* and *E. nigra* ($r = -.60$, $.05 < p < .1$).

REPRODUCTIVE EFFORT

Reproductive effort is defined as that proportion of the total energy budget of an organism that is devoted to reproductive processes (Hirshfield and Tinkle, 1975). Three questions pertain to this concept: (1) What index actually measures reproductive effort? (2) What environmental conditions act as selective factors for high and low levels of effort? (3) How are those conditions predicted?

Earlier workers (Gadgil and Bossert, 1970; Tinkle, 1969, and Tinkle, *et al.*, 1970) used ratios of clutch to body weight as measures of reproductive effort. Later workers (Ballinger and Clark, 1973; Tinkle and Hadley, 1973; Vitt, 1974; Vitt and Ohmart, 1975) emphasized the use of caloric ratios. However, Tinkle and Hadley (1975) and Hirshfield and Tinkle (1975) suggested that these ratios were inadequate, because the concept of reproductive effort, as defined by Fisher (1930), requires measurements that can be fitted to demographic models, not instantaneous values. Thus total energy budgets, incorporating data on the proportional distribution of energy to growth, maintenance and reproduction, on an age-specific basis, are necessary to assess more accurately reproductive effort at the population level (Vitt, 1978). Caloric ratios facilitate the calculation of total energy budgets for species having well known demographic parameters (Vitt, 1978). These caloric ratios are presented in Table 6 for four species of the genus *Emoia* coexisting in the same habitats on American Samoan islands, as a basis to which future demographic studies could be applied. For three of the four species with a clutch size of essentially two eggs, caloric values of relative clutch masses are significantly different (Table 6, p's $< .05$).

TABLE 6. Caloric estimates of clutch to body weight (Vitt, 1978a) for 4 coexisting species of the genus *Emoia* from islands of American Samoa.

Species	n	*Clutch size* $\bar{X}$ (Range)	*Female body weight* $\bar{X}$ (Range)	*Clutch weight* $\bar{X}$ (Range)	*Caloric value* $\bar{X}$	(95% confidence limits)
Emoia nigra	24	2.3 (1-4)	28.7 (23.6 -36.5)	3.3 (2.2 -5.7)	.419	(.409-.429)
E. samoense	7	5.3 (1-7)	22.8 (20.1 -27.5)	2.9 (2.8 -3.3)	.231	(.213-.249)
E. lawesii	4	1.8 (1-2)	18.1 (15.3 -20.6)	2.2 (1.7 -2.8)	.223	(.193-.253)
E. cyanura	34	2.0 (1.2)	2.3 (1.59- 2.9)	0.4 (.27- .52)	.276	(.276-.291)

Vitt and Congdon (1978) proposed that relative clutch masses (in terms of the caloric conversions above) are predictable on the basis of body shapes of lizards as related to certain aspects of their ecology. They proposed that the two extremes of foraging and predator escape behaviors, sit and wait foragers versus wide foragers (MacArthur and Pianka, 1966; Pianka, 1973; and Schoener, 1971), typified species with cryptic coloration and high relative clutch masses, and noncryptic coloration and low relative clutch masses, respectively. Species with contrasting combinations of behaviors and coloration (or escape strategies) were termed intermediate.

Schwaner (1979) described the ecology of the four coexisting species of *Emoia* in American Samoa, relative to resource partitioning, behavior, and morphological correlations to microhabitat preferences. *Emoia nigra* is a widely foraging terrestrial species, highly visible by its black coloration, and most wary of all the species, as demonstrated by its flight at the slightest disturbance. *Emoia samoense* exhibits the other extreme; the species is arboreal, cryptically colored (green), is much less wary than *E. nigra,* and forages in a rather limited (horizontal) area on tree trunks and in low vegetation at the bases of trees. *Emoia lawesii* is also cryptically colored, terrestrial (but confined to coral rubble substrates), and moves relatively slowly among the rocks when disturbed. *Emoia cyanura* is a small, widely foraging, semi-arboreal species, quick to escape when disturbed, with a bright blue tail which may be used as a decoy escape mechanism from predators; it would, therefore, correspond more closely to Vitt and Congdon's (1978) intermediate strategy.

When these ecological and behavioral traits are compared with the caloric ratios, the correlations are opposite of those described by Vitt and Congdon (1978) for the two extreme strategies. *Emoia nigra* the wide forager has the highest ratio, while *E. samoense* and *E. lawesii,* the cryptic, more sedentary species, have the lowest ratios. *Emoia cyanura,* with an intermediate strategy, has an intermediate caloric ratio between the two extreme groups.

Thus most lizard species in American Samoa characteristically exhibit continuous reproductive activity with slight annual variations (Sherbrooke, 1975; Duellman, 1978). In most species for which sufficient data are available, the general reproductive strategy appears to be multiple clutches annually, rather than the single clutches found in most temperate lizards (Tinkle, *et al*, 1970). Duellman (1978) stated that the reproductive strategies of lizards must be considered in terms of their phylogenetic limitations, structural habitats, and interactions with other species. The basic assumption is that clutch mass, relative to body mass, determines the agility of a gravid female lizard, and thus, her survival (and the survival of her eggs) when threatened.

In American Samoa, gekkonids exhibit a constant clutch size of two eggs, probably reflecting the inherent pattern exhibited throughout the family. Alternatively, or concommitantly, this pattern also may reflect the load-bearing limitations imposed by their arboreal habits, particularly for those species residing on building walls (Andrews and Rand, 1974). Schwaner (1979) suggested that the richest gekkonid communities on American Samoan islands are closely packed ecologically, perhaps at the point of limiting similarity (MacArthur and Levins, 1967). The reproductive modes of these species, involving low clutch size, continuous breeding activity, multiple clutches annually, resistence of eggs to dissecation, prolonged incubation times, ability to affix eggs to surfaces *(L. lugubris)*, and parthenogenetic forms (*L. lugubris* and, perhaps, *C. pelagicus*), are adaptations well suited to both colonization and maximal avoidance of competition (and resistence to predation).

The presence of another parthenogenetic species, *Cyrtodactylus pelagicus*, in American Samoa would not be surprising; *Lepidodactylus lugubris* (Cuellar and Kluge, 1972, is a known unisexual species on these islands, and two others, *Gehyra variegata* (Hall, 1970) and *Hemidactylus garnotii* (Kluge and Eckhardt, 1969) are found on nearby islands. Cuellar (1977) summarized the data concerning parthenogenetic species on islands and noted that enhancement of colonizing ability may be by prolonged sperm storage or parthenogenesis. Cuellar dismissed sperm storage as a strictly island phenomenon, since it apparently evolves on mainlands in response to other selective factors; however, prolonged incubation periods have been demonstrated for *G. oceanica* (see above), and parthenogenesis as another alternative seems ideal for American Samoan species. Their survival on these islands obviously depends in large part on how quickly their populations can respond to periodic catastrophy such as seawater innundations of lowland forests during tropical storms, volcanism, and human disturbance of lowland habitats.

Populations of *C. pelagicus* on New Guinea and adjacent islands appear to have equal sex ratios (Herbert C. Dessauer, pers. comm.). However, if populations on American Samoa are parthenogenic, the possibility of finding a male is remote. Introduction of a male into an all female population might result in matings with disruption of clones and the production of triploid offspring: if some of these triploids are males, further inbreeding would eventually build chromosome complements so high that the whole population could eventually "crash" under the "weight" of its increasing chromosome number (Jay Cole, pers. comm.).

Parthenogenesis has been found in only about 1% of the known lizard species. As a reproductive mode on islands, and in disclimax areas where few potentially competing species coexist, however, it appears a viable strategy which may be widespread in species on other islands in the Pacific region.

Among scincids in American Samoa, small skinks exhibit a constant low clutch size of two eggs, but larger skinks have, maximally, two (*E. lawesii* and *E. adspersa*), three *(E. nigra)* and seven *(E. samoense)* eggs per clutch. Small skinks exhibit small clutches probably due to the restrictions of small body size and the need for rapid escape (or protection of young in the case of *L. noctua*), as suggested by Duellman (1978) for small lizards in tropical South America. Although clutch sizes are low in small skinks, like the geckos, this may be compensated for by continuous breeding and multiple clutches annually.

Competition for small food items perhaps limits the coexistence of these forms in the same microhabitats in American Samoa (Schwaner, 1979); but, interspecific competition would seem to have little effect on reproductive modes, clutch sizes, frequency of egg deposition, patterns in annual reproductive activity, and choice of nesting sites among species so widely divergent in microhabitats. However, predation by larger lizards, birds, the Pacific boa, *Candoia bibroni,* and land crabs (feeding on eggs) may be sufficiently high to account for the differences in reproductive modes exhibited by small skinks.

The secretive and viviporous habits of *L. noctua* probably protect adults and young from predatory species. Tinkle and Gibbons (1977) reviewed the evidence supporting the evolution of viviparity in lizards. Their list of possible benefits for viviparity included: (1) protection of eggs from environmental mortality, (2) favorable thermoregulation for the developing embryos, (3) economy to the female in providing sustenance during development rather than making the entire reproductive commitment at ovulation, and (4) greater predictability in placement of newborn young in optimal sites at partuition. Not only are the secretive microhabitats of *L. noctua* often "foraged over" by other large and small scincid species (Schwaner, 1979), but also by the large gecko, *G. oceanica,* which favors nesting sites under the bark of rotting coconut stumps. The reproductive mode of *L. noctua* seems, therefore, ideally suited for a microenvironment where nesting sites may be limited; its secretive habits provide maximal separation from most other competing or predatory species. Thermoregulation could be accomplished simply by shifting to the sunny or shady sides of rotting stumps, under the bark, similar to the way *Eumeces egregius* in the Southeastern United States facilitates incubation of eggs in pocket-gopher mounds by shifting from lower to higher levels in burrows at different times of the day (Mount, 1963). *Cryptoblepharis bou-*

tonii is perhaps protected by its isolation in littoral strand habitats not explored by the larger lizard species.

But what of *E. cyanura*, which must forage and deposit its eggs in the same habitats with the larger, predatory species? Perhaps the staggered foraging times, as well as greater efficiency in handling smaller food items, intermediate foraging heights above ground, and, possibly, its tail coloration as a predator escape mechanism, contribute to the coexistence of *E. cyanura* with the larger species. The moderately high negative correlation between *E. cyanura* and *E. nigra* for their percentages of reproductively active females, could mean that *E. cyanura* has access to nesting sites also surveyed by *E. nigra,* but at different times of the year.

Among the larger species, the significant correlation between reproductive activity and mean monthly relative humidity during the day seems related to the swelling of eggs during incubation. Swelling provides at least three functions (Cunningham and Huene, 1938): (1) actual use of water by the embryo, (2) protection from external pressure on the embryo by keeping the shell fully distended, and (3) as a device for rupturing eggs (the latter function has been confirmed by these authors, and follows my own observation for the disappearance of portions of the calcareous shell at which initial rupturing of the egg occurs). Otherwise, few climatic factors seem to affect the reproductive frequencies of these species.

Like *Ameiva ameiva* in tropical South America, *Emoia nigra* may exhibit low clutch sizes due to the necessity of rapid movements (Simmons, 1975; Duellman, 1978); although there seem to be few predators capable of attacking an adult *E. nigra* on American Samoan islands, the pattern may have evolved in other areas (e.g. New Guinea) where large predators are present. Alternatively, the low number of large eggs in clutches of *E. nigra* may facilitate the placement of large, early maturing hatchlings capable of successfully competing with other small lizards (Duellman, 1978), or avoiding predation by their cannibalistic parents (Schwaner, 1979).

The large clutch size of *E. samoense* markedly contrasts with that of other large skinks on American Samoan islands. Perhaps like some arboreal species in tropical Asia (i.e., *Draco;* Inger and Greenberg, 1966) and South America (i.e., *Enyalioides laticeps;* Duellman, 1978), *E. samoense* is sufficiently isolated by microhabitat that its reproductive habits are generally not affected by the interspecific interactions that apparently limit clutch size in other, more terrestrial skinks.

Thus, the positive correlation between monthly reproductive frequencies of *E. nigra* and *E. samoense* does not necessarily imply overlap in nesting sites. The predation by *E. nigra* on *E. samoense* eggs noted above may be an exceptional case, taking place in mangrove forest where nesting sites are obviously more limited for the terrestrial species. Alternatively, if *E. samoense* eggs are laid in arboreal nests, these sites may be sensitive to adverse ambient weather conditions, thus, limiting their favorability to the developing eggs. The eggs of *E. samoense* must also absorb water. This necessity may be indicated by the negative correlation between reproductive frequencies and duration of daylight, because months with shorter days are also highly correlated with maximal rainfall and low wind speed. This could assure that such potential nesting sites as epiphytic birdnest ferns are saturated with water and less prone to drying by wind. Perhaps the apparent retention, or prolonged development, of ova by *E. samoense* is also related to the limitations of available nesting sites in arboreal habitats. If the eggs are laid singly (which must be determined by further study) more time would be required in finding suitable nests.

The lengthy incubation period of *E. lawesii* eggs may simply reflect the cooler environments in which the eggs are placed, assuming that these nests are under the layers of coral plates to which the species is apparently restricted. The markedly lower active foraging temperatures of *E. lawesii* than for all other scincid species in American Samoa (Schwaner, 1979) may be related to egg development at these presumably low temperatures.

The general conclusion for most American Samoan lizards seems to suggest that their reproductive strategies reflect adaptations more for avoidance of interspecific interactions than for climatic variables which greatly influence other species in seasonal temperate and equatorial tropical areas.

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LITERATURE CITED

AMERSON, A. B., JR., A. C. WHISTLER, T. D. SCHWANER. 1978. An inventory of the wildlife and wildlife habitat of the islands of American Samoa. Vols. I, II, III, 813 pp. Environment Consultants, Inc., 14325 Proton Road, Dallas, Texas 75240 (unpublished).

ANDREWS, R., A. S. RAND. 1974. Reproductive effort in anoline lizards. Ecology, 55: 1317-1327.

BAKER, J. R. 1947. The seasons in a tropical rain-forest. Part 6. Lizards *(Emoia).* Jour. Linn. Soc. London, 41 (no. 279): 243-247.

BALLINGER, R. E., D. R. CLARK. 1973. Energy content of lizards eggs and the measurement of reproductive effort. J. Herpetol. 7: 129-132.

BROWN, K. M., O. J. SEXTON. 1973. Stimulation of reproductive activity of female *Anolis sagrei* by moisture. Physiol. Zool. 46: 168-172.

BROWN, W. C. 1956. The distribution of terrestrial reptiles in the islands of the Pacific Basin. Proceedings of the Eighth Pacific Science Congress, 3A: 1479-1491.

BROWN, W. C., A. C. ALCALA. 1957. Viability of lizard eggs exposed to sea water. Copeia, 1957, (1): 39-41.

CAGLE, F. R. 1946. A lizard population on Tinian. Copeia, 1946 (1): 4-9.

CHURCH, G. 1962. The reproductive cycles of the Javanese house geckos, *Cosymbotus platyurun, Hemidactylus frenatus,* and *Peropus mutilatus.* Copeia, 1962 (2): 262-269.

COLWELL, R. K. 1974. Predictability, constancy, and contingency of periodic phenomena. Ecology 55(5): 1148-1153.

CRUMP, M. L. 1974. Reproductive strategies in a tropical anuran community. Misc. Publ. Mus. Nat. Hist. Univ. Kansas, (61): 1-68.

CUELLAR, O. 1977. Animal parthenogenesis. Science, 197: 836-843.

CUELLAR, O., A. G. KLUGE. 1972. Natural parthenogenesis in the gekkonid lizard *Lepidodactylus lugubris.* Jour. Genet. 61(1): 14-28.

CUNNINGHAM, B., E. HUENE. 1938. Further studies on water absorption by reptile eggs. Am. Nat. 72: 380-385.

DUELLMAN, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. Misc. Publ. Mus. Nat. Hist. Univ. Kansas, (65): 1-352.

FISHER, R. A. 1930. The genetical theory of natural selection. Am. Natur. 104: 1-24.

FITCH, H. S. 1954. Life history and ecology of the five-lined skink, *Eumeces fasciatus.* Univ. Kansas Publ. Mus. Nat. Hist., 8 (1): 1-156.

FITCH, H. S. 1956. An ecological study of the collared lizard *(Crotaphytus collaris).* Univ. Kansas Publ. Mus. Nat. Hist., 8 (3): 213-274.

FITCH, H. S. 1970. Reproductive cycles in lizards and snakes. Misc. Publ. Mus. Nat. Hist. Univ. Kansas, (52): 1-247.

FITCH, H. S. 1972. A field study of Costa Rican lizards. Univ. Kansas Sci. Bull., 50 (22): 39-126.

FITCH, H. S., H. W. GREENE. 1965. Breeding cycle in the ground skink, *Lygosoma laterale.* Univ. Kansas Publ. Mus. Hist., 15 (11): 565-575.

FUGLER, C. M. 1966. *Lepidodactylus lugubris* Dumeril and Bibron in Western South America. Jour. Ohio Herp. Soc., 5: 162.